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Fishery Bulletin

Vol. 83, No. 1 January 1985

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Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is also available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115. Second class postage is paid at Seattle, Wash., and additional offices. POSTMASTER send address changes for subscriptions to Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

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The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 1 April 1985.

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THE ROCK SHRIMP GENUS *SICYONIA* (CRUSTACEA: DECAPODA: PENAEOIDEA) IN THE EASTERN PACIFIC

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The genus *Sicyonia* is redefined and the 12 species occurring between Monterey Bay, California, and off Pisco, Peru, are treated in detail. A key to species is followed by illustrated species accounts including descriptions, ranges of intraspecific variation with analyses of morphometric data (rostrum to carapace ratio graphically represented for 10 species), and color notes. The size ranges at which males and the minimum sizes at which females attain adulthood are summarized, and ecological notes together with maps illustrating the ranges of the species (six of which have been extended beyond limits previously reported) are included. *Sicyonia disparri* seems to be restricted to the south and gulf coasts of Baja California and waters off Nayarit, Mexico; *S. affinis* to waters off Costa Rica, Panama, and Colombia; and *S. penicillata* occurs on the ocean side of Baja California Sur, Mexico, and from the Gulf of California to Costa Rica. *Sicyonia ingentis* ranges from Monterey Bay to Nayarit, including the Gulf of California. *Sicyonia disedwardsi* and *S. martini* occur along the ocean side of Baja California Sur, in the Gulf of California, and southward to Panama, and four others, *S. aliaffinis*, *S. disdorsalis*, *S. mixta*, and *S. picta*, frequent the same waters, but also reach as far south as Peru. *Sicyonia laevigata* and *S. brevirostris* are found on both sides of the Continent, the former at the southern end of the Gulf of California and from off Costa Rica to the Golfo de Panamá in the Pacific, and from North Carolina to Santa Catarina, Brazil, in the Atlantic. *Sicyonia brevirostris* has been recorded from the Golfo de Tehuantepec and from Virginia southward through the Gulf of Mexico to Yucatán, and also from the Bahamas and Cuba. In addition, there is an unverified literature record from Guyana. The treatment of each species is concluded with a comparison of its diagnostic features with those of the most closely allied congeners and a note on its present or potential economic value.

Until a few years ago, members of the genus *Sicyonia*, "rock shrimps", were discarded from the large commercial catches of panaeoid shrimps made in tropical and subtropical waters of the eastern Pacific and western Atlantic. It was commonly thought that because of their hard, stony exoskeleton, they would be rejected by both consumers and the processing industry; however, increased demand for shrimp encouraged the fishermen and dealers to bring the larger species to market, and now production is not only readily absorbed, but some prefer rock shrimps to the thinner shelled species.

The exploitation and comparatively recent recognition of the commercial potential of *Sicyonia*, the most distinctive group within the superfamily Penaeoidea, have motivated this review of members of the genus found in the American Pacific (the western Atlantic species have already been the object of a number of studies, e.g., Chace 1972; Huff and Cobb 1979). For the most part, the information available is limited to the original descriptions of the species, which are scattered in works published between 1871 and 1945, and to a limited number of locality records. Of the 12 species occurring in the region, 4 had been recognized prior to the close of the century. No other species were reported from these waters until Burkenroad made his invaluable studies (1934-45) which resulted in the recognition of five new species plus two others previously known to occur only in the western Atlantic. Recently, Pérez Farfante and Boothe (1981) described the 12th member of the genus frequenting the eastern Pacific. Two works have been helpful in the identification of the American *Sicyonia*: one by Anderson and Lindner (1945) which provided a key to the then known species; the other by Arana Espina and Méndez G. (1978) in which was presented an illustrated key, diagnoses, and ranges of the species found in Peruvian and Ecuadorean waters, and an analysis of morphometric relations, with data on the growth and molting pattern of one of the species.

The extensive collections (515 lots containing 4,672 specimens) of *Sicyonia* available from Monterey Bay, Calif., to off Pisco, Peru, and the oppor-

[1]Systematics Laboratory, National Marine Fisheries Service, NOAA, National Museum of Natural History, Washington, DC 20560.

Manuscript accepted April 1984.
FISHERY BULLETIN: VOL. 83, NO. 1, 1985.

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tunity to examine all except two of the extant type-specimens of the species have made a critical study of the genus in the eastern Pacific possible. The present work includes a definition of the genus and a key to the species occurring in the region. A complete synonymy and usually complete list of references, vernacular names, and a diagnosis precede the detailed description of each species, which includes a discussion of the extensive variation exhibited as well as meristic and morphometric data. In addition, relation of the length of the rostrum to the length of the carapace is graphed for 10 species. Color notes, size range at which males reach adulthood, and minimum size at which females have been observed to be impregnated are given. Geographic and bathymetric ranges are delimited, and ecological data are provided. Analyses of the diagnostic features utilized in the recognition of species and a discussion of their phylogenetic relationships are also presented. Distributional maps as well as illustrations of entire animals, genitalia, and a few other morphological features are included along with a bibliography which is as complete as possible. A statement of their economic importance follows the treatment of the pertinent species, and a list of the specimens examined, with their localities, is appended to each of the 12 species.

The distributional studies have resulted in extensions of both geographic and bathymetric ranges of several species; e.g., of the seven species known to occur both in the Gulf of California and on the ocean side of the peninsula, five have not been previously reported from the latter, and one, which had been recorded only as far north as Point Conception, Calif., was found to reach Monterey Bay (Pérez Farfante and Boothe 1981). Of the 12 species that have been reported from the region, 10 (or 11, in the unlikely event that the presence of *S. affinis* is confirmed) occur in the Gulf of California; of those occurring in the gulf, *S. disparri* appears to be virtually confined to it and only *S. ingentis* extends northward beyond Mexico, along the coast of the United States. Eight of the 10 species range southward to Central America, and of them 4 reach as far as Peru and *S. aliaffinis* also occurs off Islas Galápagos. *Sicyonia brevirostris* has been reported exclusively from the Golfo de Tehuantepec, and *S. affinis* is known with certainty only from Costa Rica to Colombia.

Seven of the species, *S. laevigata, S. mixta, S. disedwardsi, S. penicillata, S. aliaffinis, S. martini,* and *S. picta*, appear to have disjunct ranges. None has been recorded from stretches variable in extension within the limits cited herein, and all of the gaps encompass areas off southern Mexico. Perhaps the discontinuities are due to limited exploratory investigations; however, one species, *S. disdorsalis*, has been found to occur virtually continuously from the Gulf of California to Peru. Nevertheless, speculations attempting to explain the apparent gaps in the ranges of these species should await the confirmation of their existence.

Except for records of the occurrence of *S. picta* at 333 m (Faxon 1893) and 369-400 m (Arana Espina and Méndez G. 1978) and *S. brevirostris* at 329 m (Williams 1965), no other species were previously known from depths greater than about 200 m; here six others are reported between about 250 and 300 m, depths considerably greater than their previously known maximum occurrence.

Distributions of members of the genus *Sicyonia* in the eastern Pacific appear to differ strikingly from those of most species of the closely related family Penaeidae in that region. Whereas some species of *Sicyonia* are restricted to comparatively small areas (one confined to the southern and gulf coasts of Baja California and waters immediately south), others range from the Gulf of California to the northern or to the central coasts of Peru. Most of the eastern Pacific species, like their western Atlantic congeners, reveal a marked preference for firm or coarse bottoms.

PRESENTATION OF DATA

Many characters used in the descriptions are depicted in Figures 1-7. To provide an appreciation of the structure of the eye and the nomenclature employed in its description I have chosen that of *S. disedwardsi*. To illustrate the first article of the antennular peduncle and anterior gnathal appendages, *S. ingentis* was selected. The petasmata have been drawn from specimens stained with fast green. For convenience, both the armature of sternite XI and the shape of the posterior thoracic ridge are presented with the description of the thelycum. Scales accompanying the illustrations are in millimeters. The length of the rostrum (rl) recorded herein is the linear distance from the apex to the orbital margin; length of the carapace (cl) is the distance between the orbital margin and the midposterior margin of the carapace; and the total length (tl) is the distance from the apex of the rostrum to the posterior end of the telson. The geographic distribution of each of the species presented on the maps is based on material personally examined and on published records believed to be

reliable. The names of the countries cited are in English as are the Gulf of California and the Gulf of Mexico; otherwise, all geographic features and localities are in the language of the country in which they occur.

Material examined during this study are in the collections of the following institutions.

AHF	Allan Hancock Foundation, Los Angeles, California, USA
AMNH	American Museum of Natural History, New York, New York, USA
CAS	California Academy of Sciences, San Francisco, California, USA
IMARPE	Instituto del Mar del Perú, Callao, Peru
INP	Instituto Nacional de Pesca, Secretaría de Pesca, México D.F., Mexico
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MP	Muséum National d'Histoire Naturelle, Paris, France
SIO	Scripps Institution of Oceanography, La Jolla, California, USA
UCR	Universidad de Costa Rica, San José, Costa Rica
UP	Universidad de Panamá, Panama
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA
ZMB	Zoologisches Museum der Humboldt-Universität, Berlin, East Germany.

Genus *Sicyonia* H. Milne Edwards 1830

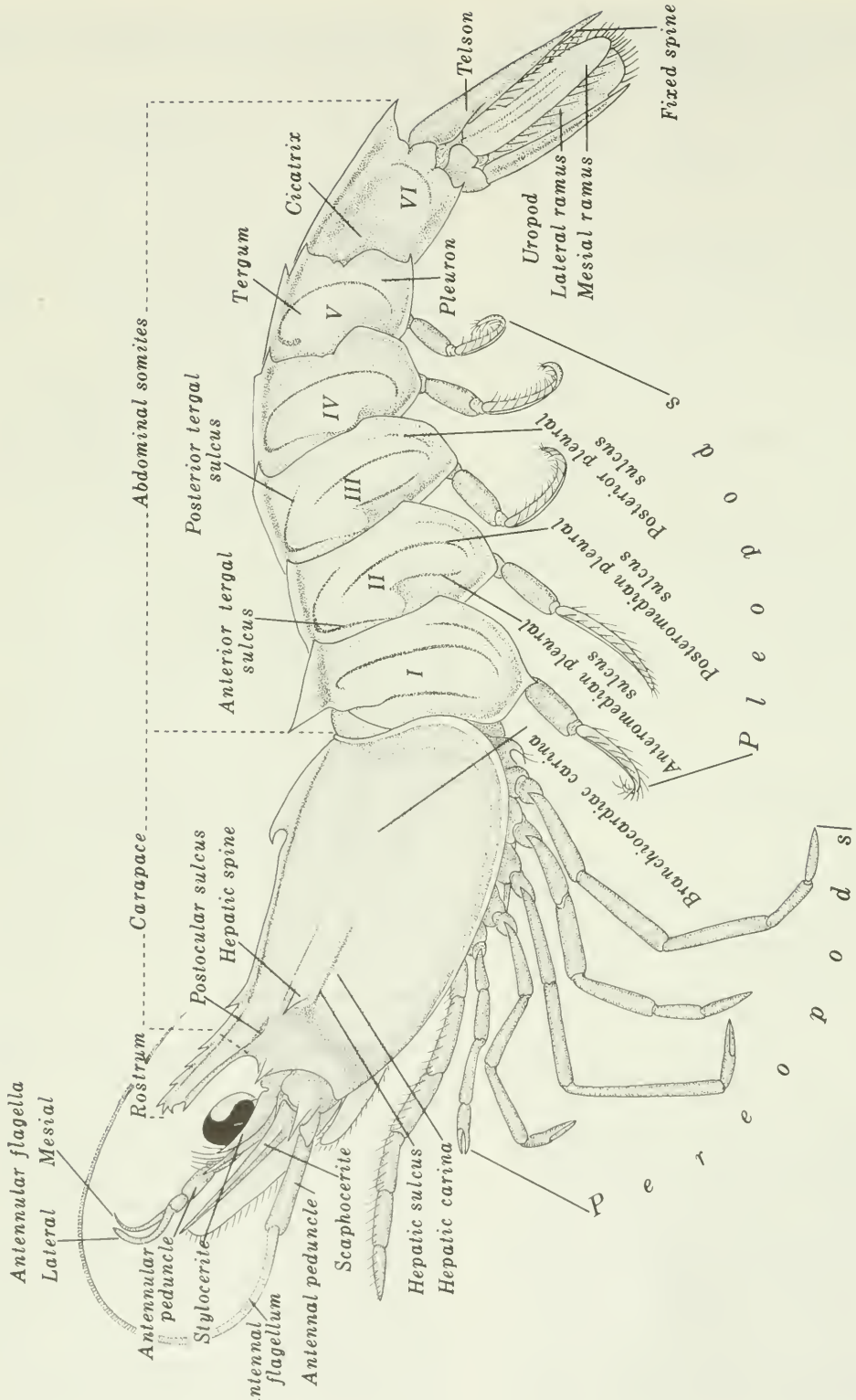
Sicyonia H. Milne Edwards 1830:339 [type-species, by monotypy: *Sicyonia sculpta* H. Milne Edwards 1830:340 (= *Cancer carinatus* Brünnich 1768:102)]. H. Milne Edwards 1837:408. De Haan 1849:187. Heller 1863:290. Bate 1888:292. A. Milne Edwards and Bouvier 1909:243. Balss 1914:14. Burkenroad 1945:1. Barnard 1950:635. Holthuis 1952:339. Hall 1956:87. Zariquiey Alvarez 1968:57. [Name validated and placed on the Official List of Generic Names in Zoology as Name No. 922 under Plenary Powers of the International Commission on Zoological Nomenclature, Opinion 382, 1956:45; Hemming 1958:126.] Gender: feminine.

Ruvulus de Natale 1850:20 (published as synonym of *Sicyonia* H. Milne Edwards 1830) [type-species, by monotypy for *Sicyonia* H. Milne Edwards: *Sicyonia sculpta* H. Milne Edwards 1830]. Holthuis 1952:339. Hall 1956:87. Gender: masculine.

Synhimantites Boeck 1864:189 [type-species, by monotypy: *Synhimantites typicus* Boeck 1864:189]. Burkenroad 1945:1. Holthuis 1952:339. Gender: masculine.

Eusicyonia Stebbing 1914:25 (substitute name for *Sicyonia* H. Milne Edwards 1830) [type-species, by monotypy for *Sicyonia* H. Milne Edwards 1830: *Sicyonia sculpta* H. Milne Edwards 1830]. Balss 1925:232. Burkenroad 1934a:70, 1934b:116, 1945:1. Kubo 1949:437. Holthuis 1952:339. Hall 1956:87. Gender: feminine.

Diagnosis.—Body with integument rigid, microscopically setose-punctate. Rostrum short, not overreaching distal margin of antennular peduncle, more often falling short of it, and armed with dorsal, and usually apical teeth, lacking ventral ones (Fig. 1). Carapace with postrostral carina bearing epigastric tooth and variable number of teeth more posteriorly; orbital, postorbital, and pterygostomian spines lacking; antennal spine present or absent; hepatic spine well developed; cervical sulcus indistinct; hepatic sulcus usually shallow; hepatic carina weak or indistinct; branchiocardiac carina strong to barely distinct (Fig. 2). Abdomen marked by transverse sulci bordered by closely set setae; dorsomedian carina extending for entire length; carina on first somite usually produced in large anterior tooth, that on second incised or entire, and that on sixth terminating in strong tooth; sixth somite bearing cicatrix. Telson armed with pair of marginal, fixed, subterminal spines. Optic calathus articulated directly to basal article of eyestalk, intermediate article [= Young's (1959) optic stalk] not apparent; ocular stylet projecting from anterolateral margin of ocular plate (Fig. 3). Antennular peduncle about 0.6 cl; prosartema (Fig. 4*F-p*) rudimentary; stylocerite long, produced as sharp spine; antennular flagella short, not exceeding 0.5 cl, mesial flagellum tapering gradually from base, lateral one broad from base to near tip, then tapering rapidly to apex. Mandibular palp (Fig. 4*A*) three-jointed, proximal article small and short, distal article large, much larger than penultimate one, and roughly


Antennular flagella
Lateral
Mesial
Rostrum
Carapace
Abdominal somites
Postocular sulcus
Hepatic spine
Antennular peduncle
Stylocerite
Antennal flagellum
Antennal peduncle
Scaphocerite
Hepatic sulcus
Hepatic carina
Posterior tergal sulcus
Anterior tergal sulcus
Tergum
Cicatrix
Pleuron
Telson
Uropod
Lateral ramus
Mesial ramus
Fixed spine
I
II
III
IV
V
VI
Pereopods
Pleopods
Anteromedian pleural sulcus
Posteromedian pleural sulcus
Posterior pleural sulcus
Branchiocardiac carina

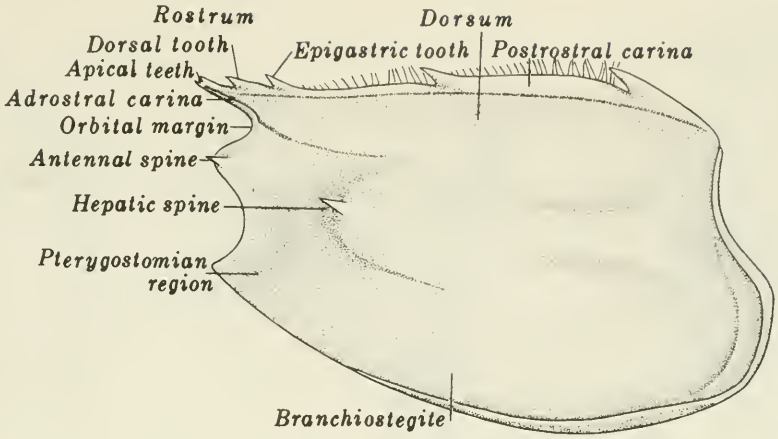


FIGURE 2.—Lateral view of carapace of *Sicyonia* showing terms used in descriptions.

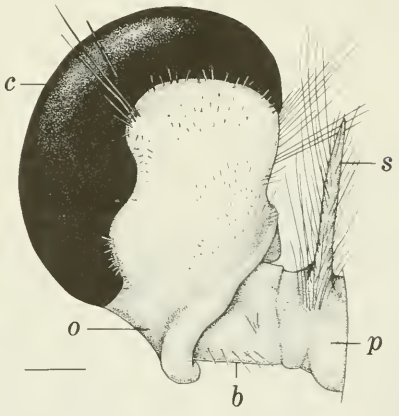


FIGURE 3.—*Sicyonia disedwardsi* Stimpson, ♀ 30 mm cl, Golfo de Panamá, Panama. Eye, dorsal view: *b*, basal article; *c*, cornea; *o*, optic calathus; *p*, ocular plate; *s*, ocular stylet. Scale = 1 mm.

trapezoidal; first maxilla (Fig. 4*B*) with broad palp unjointed and not produced distally; second maxilla (Fig. 4*C*) with basipodite lacking proximal gnathal lobule; first maxilliped with flagellum quite short (Fig. 4*D*); second maxilliped as illustrated (Fig. 4*E*). Exopods lacking on second and third maxillipeds and all pereopods. First pereopod unarmed or with mesial spine on basis and ischium. Endopods of pleopods absent except for highly modified ones on first (petasma) and second (bearing appendix masculina) pleopods. Petasma (Fig. 5*A*) depressed, with dorsolateral and heavily cornified ventrolateral lobules produced in distal projections, that of former funnel-like, and with ventromesial slit; distal part of dorsomedian lobule bearing short distal plate resembling cusp in ventral aspect. Appendix masculina (Fig. 5*B*) projecting from free distal part of ridge on dorsomedian margin of endopod, small, roughly bellshaped, but with membranous terminal wall. Male gonopores situated on sternite XIV. Thelycum (Fig. 6) with plate of sternite XIV single, flat or raised in paired, weak or prominent, lateral bulges. Paired seminal receptacles (Fig. 7)

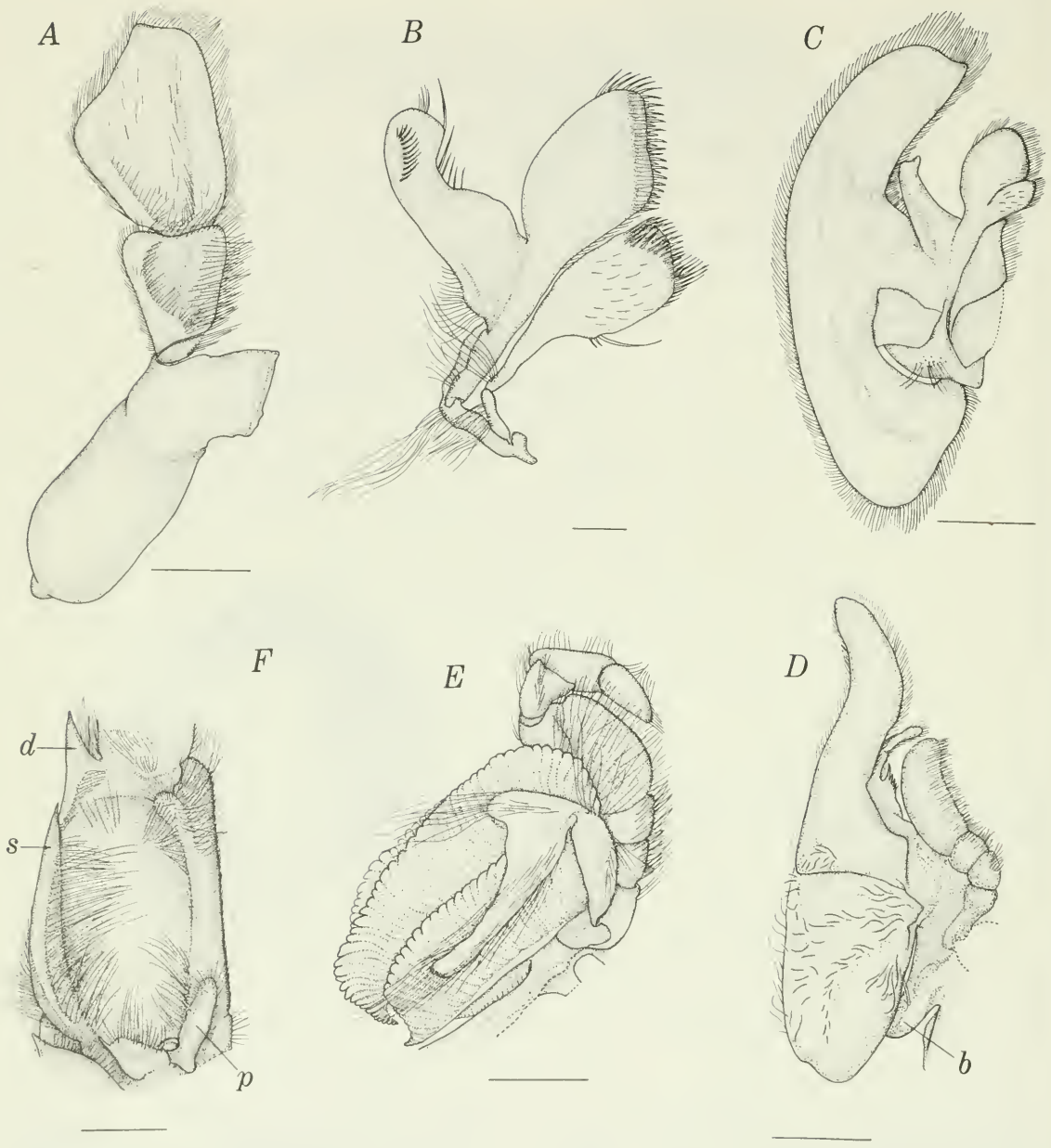


FIGURE 4.—*Sicyonia ingentis* (Burkenroad 1938), ♀ 38 mm cl, off Bahía de San Quintín, Baja California Norte, Mexico. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *D*, First maxilliped—*b*, branchial rudiment (arthrobranchia). *E*, Second maxilliped. *F*, First article of antennular peduncle—*d*, distolateral spine; *p*, rudimentary prosartema; *s*, stylocerite. Scales: *A*, *C-E* = 3 mm; *B* = 1 mm; *F* = 3 mm.

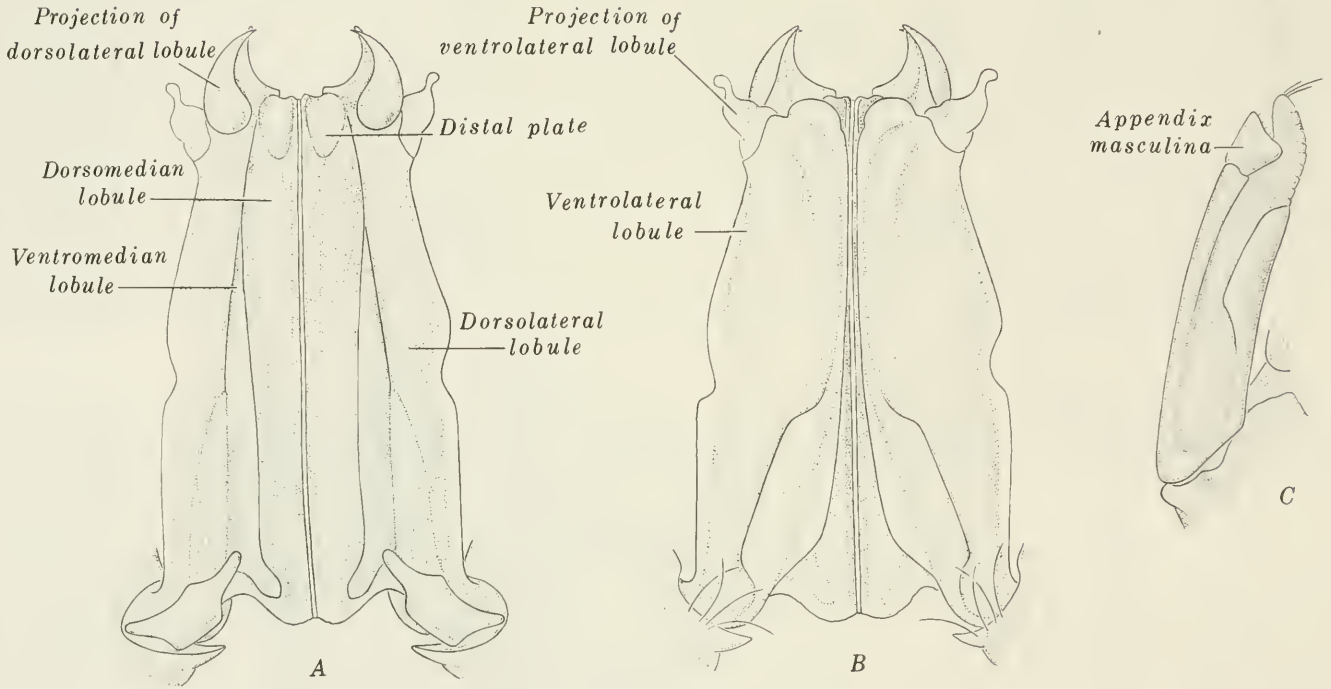


FIGURE 5.—*Sicyonia disparri* (Burkenroad 1934), ♂ 6 mm cl, Canal de San Lorenzo, Baja California Sur, Mexico. *A*, Dorsal view of petasma showing terms used in descriptions; *B*, ventral view of same; *C*, dorsolateral view of appendix masculina on second pleopod.

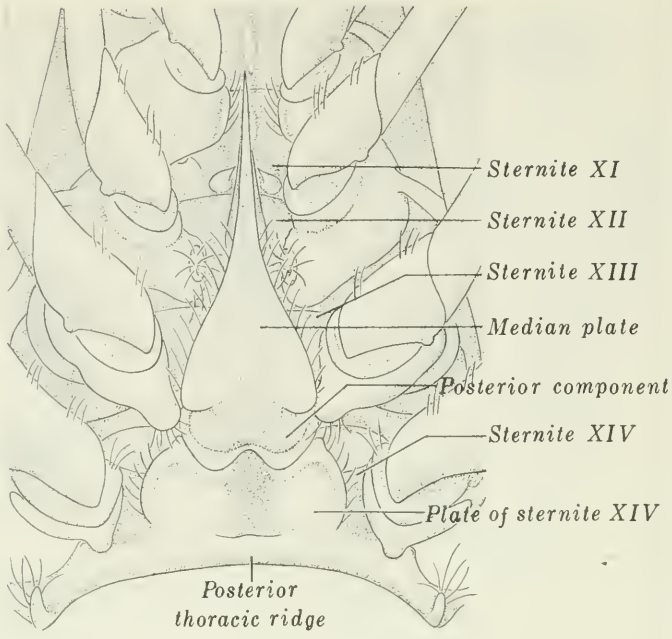


FIGURE 6.—Thelycum of *Sicyonia* showing terms used in descriptions.

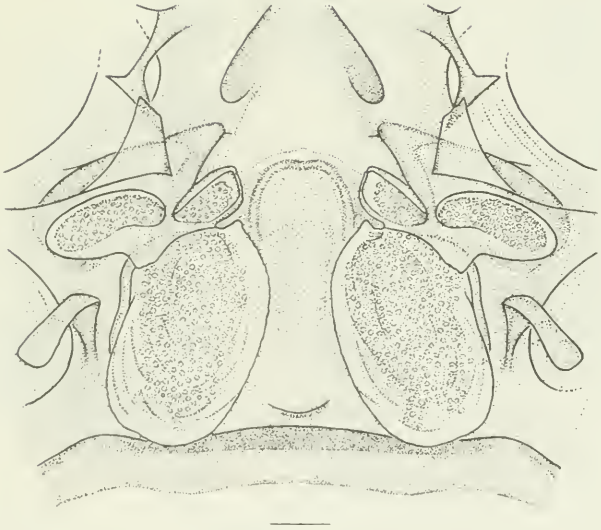


FIGURE 7.—*Sicyonia disedwardsi*, ♀ 30 mm cl, Golfo de Panamá, Panama. Dorsal view of sperm receptacles. Scale = 1 mm.

consisting of trilobed membranous sacs: large, longitudinally disposed, mesial lobe, extending to posterior margin of sternite XIV, and two small anterior lobes, one directed anteriorly and the other laterally; receptacles opening by transverse slits at anterolateral margins of plate of sternite XIV. Median plate of sternite XIII (supported by buttress of sternite XII) large, triangular or flask-shaped, tapering anteriorly in long, sharp spine; plate bearing well-defined lateral constrictions setting off posterior component. Sternite XI armed posteriorly with paired spines of variable size. Branchial components consisting of pleurobranchia on somite IX; single arthrobranchia on somite VII (lamellar rudiment; Fig. 4*D-b*); anterior and posterior arthrobranchiae on somites VIII through XIII, anterior member of VIII very small and that of XIII vestigial; and podobranchia

on second maxilliped. Epipod on first and second maxillipeds and on first through third pereopods. [Modified from Burkenroad (1934a, b) and Kubo (1949).]

The species of this genus (about 55), the only one encompassed in the family Sicyoniidae, occur in tropical, subtropical, and temperate waters. They are marine, some invading brackish waters, and abundant at shallow to moderate depths; a number of them also range across the continental shelf onto the upper slope, reaching depths of several hundred meters.

Members of *Sicyonia* exhibit a wide range of intraspecific variation. The number and position of the dorsal and apical rostral teeth and the arrangement of teeth on the postrostral carina vary as do the depth, extension, and form (continuous or interrupted) of the abdominal sulci. Although the number of the latter almost always provide a reliable diagnostic character for specific identification, the posterior pleural sulcus may be present or absent in some species. Furthermore, in females the contour and sculpture of the thelycal plate of sternite XIV and the shape of the posterior margin of that of XIII also vary as pointed out in the accounts for most of the species. In contrast, the petasma of each of the members of the genus is virtually invariable and thus useful for specific recognition, and the appendix masculina is almost constant in shape in all of the species.

In the females, sternite XI is armed with a pair of spines which vary considerably in length, ranging from quite small, as in all members of *Sicyonia* occurring in the eastern Pacific, to extremely long, as in the western Atlantic *S. olgae* Pérez Farfante 1980. The posterior thoracic ridge varies but within a range that does not prevent its having at least limited diagnostic value.

Species of *Sicyonia* also exhibit various morphological changes with increasing size. The shape of the anteroventral margin of the pleuron of the first abdominal somite may change gradually from straight in juveniles to pronouncedly concave in adults, and the anteroventral extremities of the pleura of the first three or four abdominal somites, from rounded to sharply acute. The pleural armature, too, undergoes modifications with age; as Burkenroad (1934a) stated, "A rounded angle usually precedes an unarmed but acute angle, and this a veritable tooth, in the course of individual development"; likewise, the abdominal sculpture is altered, the sulci usually becoming deeper as the animal grows. The foregoing statements indicate that abdominal features which are diagnostic for the identification of adults have scant systematic usefulness in identifying juveniles.

Another characteristic of the genus is the wide range in size among the species; whereas some are small (the eastern Pacific *S. disparri* reaches a maximum total length of about 44 mm), others are quite large (*S. ingentis* and *S. brevirostris* attain a total length of about 133 and 153 mm, respectively).

In the genus *Sicyonia* there are two series of species the contrasting characters of which would appear to justify their separation into two genera. The members of one series (occurring on both sides of the Atlantic, in the Mediterranean and Indo-Pacific, and represented in the eastern Pacific by *S. disparri* and *S. laevigata*) lack or occasionally exhibit a very minute antennal spine, are armed with basial and ischial spines on the first pair of pereopods, bear an incision or a notch on the dorsomedian carina of the second abdominal somite, and usually display a conspicuous notch on the lateral margin of the petasma. The members of the other series (restricted to American waters) have a well-developed, buttressed, antennal spine, lack basial and ischial spines on the first pair of pereopods, have no incision on the carina of the second abdominal somite, and never bear a notch on the lateral margin of the petasma. These two series, representing extremes of the range of variation in members of the genus, were first recognized by Burkenroad (1934a) as Division I and Division II, respectively. Both in 1934a and 1945, he stated that there are species or series of species in which some of these characters are interchanged. Certain species (all from the Indo-Pacific) that lack an antennal spine and in which the first pair of pereopods are armed exhibit an entire carina on the second abdominal somite (the first two are characters of Division I, and the last of Division II). At least one species (also occurring in the Indo-Pacific) lacks an antennal spine and has armed first pereopods (both characters of Division I) but bears an unnotched carina (a feature of Division II). Another species (the eastern Pacific *S. mixta*) that possesses an antennal spine and has armed first pereopods exhibits a clearly distinct depression on the carina of the second abdominal somite which seems to correspond to the notch characteristic of Division I.

Burkenroad (1934a) also divided his Division II into species-groups, each named for one of the species belonging to it. They were characterized by the number, size, and position of the teeth on the

postrostral carina. The complex intergradation of the characters that have been used to recognize these "Divisions" and "groups" of *Sicyonia* seems to demonstrate that there are no superspecific disjunctions that will justify their being accorded subgeneric or generic rank. In the present work, occasionally, reference is made to these subdivisions.

Key to the American Pacific species of *Sicyonia*

1a. First abdominal somite lacking tooth on dorsomedian carina ..... *S. mixta*
1b. First abdominal somite bearing anterior tooth on dorsomedian carina 2

2a. Antennal spine absent or exceedingly weak and without buttress; second abdominal somite with perpendicular incision in anterior half of dorsal carina; first pereopod with short distomesial spine on basis and ischium 3
2b. Antennal spine well developed and buttressed; second abdominal somite not incised; first pereopod with basis and ischium unarmed 4

3a. Postrostral carina armed with 3 subequal teeth, anterior (epigastric) one as large, or almost as large, as posterior 2 teeth; anteromedian sulcus of first abdominal somite well marked to near ventral margin of pleuron; posteroventral extremity of fourth abdominal somite distinctly angular ..... *S. disparri*
3b. Postrostral carina armed with 3 unequal teeth, anterior one conspicuously smaller than posterior 2 teeth; anteromedian sulcus of first abdominal somite short, often obscure, ending well above ventral margin of pleuron; posteroventral extremity of fourth abdominal somite never distinctly angular ..... *S. laevigata*

4a. Postrostral carina with 2 or 3 teeth posterior to level of hepatic spine 5
4b. Postrostral carina with 1 tooth posterior to level of hepatic spine 7

5a. Postrostral carina almost always with 3 teeth posterior to level of hepatic spine, occasionally anterior one of these at level of or slightly anterior to hepatic spine ..... *S. brevirostris*
5b. Postrostral carina with 2 teeth posterior to level of hepatic spine, never with tooth at level or slightly anterior to hepatic spine 6

6a. Rostrum bearing 2 dorsal teeth; petasma with distal projections short and stout; thelycum with plate of sternite XIV raised in low (sometimes indistinct) bulges and with posterior component of median plate traversed by weak suture; branchiostegite with large ocellus consisting of well-defined yellow center surrounded by purplish brown ring ..... *S. disedwardsi*
6b. Rostrum usually bearing 1 dorsal tooth (rarely 2); petasma with distal projections extremely long and slender; thelycum with plate of sternite XIV raised in strong bulges and with posterior component of median plate traversed by deep groove; branchiostegite with moderately large, purplish brown spot sometimes bearing poorly defined but diffuse yellow center ..... *S. penicillata*

7a. Postrostral carina behind posterior tooth high, conspicuously elevated in arched crest 8
7b. Postrostral carina behind posterior tooth low, not elevated in high crest 11

8a. Fifth abdominal somite without tooth or sharp angle at posterior end of dorsomedian carina; anteroventral extremity of pleuron of fourth abdominal somite broadly obtuse and unarmed ..... *S. affinis*
8b. Fifth abdominal somite with tooth or sharp angle at posterior end of dorsomedian carina; anteroventral extremity of pleuron of fourth abdominal somite sharply angular or armed with spine 9

9a. Rostrum long, conspicuously surpassing distal margin of eye; anteroventral angle of second through fourth abdominal somites unarmed, lacking spine; petasma with projection of dorsolateral lobule distinctly bifurcate apically ..... *S. martini*
9b. Rostrum short, falling short of, or infrequently barely surpassing distal margin of eye; anteroventral angle of second

through fourth abdominal somites armed with curved spine; petasma with projections of dorsolateral lobule simple 10

10a. Rostrum armed with 2 dorsal teeth; abdomen heavily tuberculate; anteromedian pleural sulcus of first abdominal somite well marked to near ventral margin of pleuron; anteromedian pleural sulcus of second and third somites reaching dorsally posteromedian pleural sulcus; branchiostegite with horizontally disposed 9-shaped, brown mark ..... *S. aliaffinis*

10b. Rostrum armed with 3 or 4 dorsal teeth; abdomen with very few tubercles; anteromedian pleural sulcus of first abdominal somite well marked only dorsally; anteromedian pleural sulcus of second and third somites not reaching dorsally posteromedian pleural sulcus; branchiostegite with ocellate mark, consisting of red center surrounded by yellow ring ..... *S. picta*

11a. Dorsomedian carina of first abdominal somite produced in tooth considerably larger than posterior tooth on carapace, that of fifth truncate or produced in spine at posterior end; petasma with distal projections of dorsolateral lobules turned mesially and lacking terminal filament; thelycum with posterior component of median plate flat or slightly raised posterolaterally, not bearing short bosses cut by transverse suture ..... *S. disdorsalis*

11b. Dorsomedian carina on first abdominal somite produced in tooth smaller or only slightly larger than posterior tooth on carapace, that of fifth sloping gradually to posterior end; petasma with distal projections of dorsolateral lobules divergent and produced in short filament; thelycum with posterior component of median plate bearing paired short lateral bosses cut by transverse suture ..... *S. ingentis*

Sicyonia laevigata Stimpson 1871

Figures 8-12

Sicyonia laevigata Stimpson 1871: 131 [type not extant; type-locality: Charleston, S.C.]. Kingsley 1878:69, 1880:426. Rathbun 1901: 103 [part]. De Man 1911:11. Bouvier 1918:6. Hay and Shore 1918:379, pl. 25, fig. 1. Rathbun 1920:319. Burkenroad 1945:5. Lunz 1945:4, fig. 1. Pearse and Williams 1951: 143. Wass 1955:142. Menzel 1956:41. Hutton et al. 1959:6. Wells 1961:248. Williams 1965:33. Fausto Filho 1966a:32, 1966b:47, fig. 8. Eldred et al. 1965:32. Joyce and Eldred 1966:24. Fausto Filho 1968:73. Rouse 1969:136. Bayer et al. 1970:41. Lyons et al. 1971:28. García Pinto 1971:5. Chace 1972:11. Camp et al. 1977:23. Rodríguez de la Cruz 1977:11. Huff and Cobb 1979:67, fig. 38a-d. Rodríguez 1980:70. Pérez Farfante 1980:773. Greening and Livingston 1982:151. Coen and Heck 1983:206. Williams 1984:47.

Sicyonia sculpta var. *americana* De Man 1907:450.

Sicyonia carinata De Man 1907:451. [Not *Cancer carinatus* Brünnich 1768 = *Sicyonia carinata*.]

Sicyonia carinata var. *americana* De Man 1911:10.

Eusicyonia laevigata. Burkenroad 1934a:76, fig. 21, 26, 32, 1934b:117. Schmitt 1935:132. Burkenroad 1938:80. Lunz 1945:4, fig. 1.

Sicyonia carinata americana. Burkenroad 1934a:76.

Vernacular names: rock shrimp, hardback, coral shrimp (United States); camarón de piedra, cacahuete (Mexico); camarón conchiduro (Mexico, Panama); camarão-da-pedra (Brazil).

Diagnosis.—Antennal spine absent or barely distinct and lacking buttress. Second abdominal somite with perpendicular incision on dorsomedian carina. First pereopod armed with short spine on basis and ischium. Postrostral carina bearing three unequal teeth, epigastric one considerably smaller than posterior two teeth. Anteromedian sulcus of first abdominal somite, if distinct, short, ending well above margin of pleuron; posteroventral extremity of fourth abdominal somite not distinctly angular. Petasma with distal projection of dorsolateral lobule almost straight but with apical part curved dorsally. Thelycum with plate of sternite XIV produced in elongate anterolateral lobules, their anteromesial borders strongly divergent.

Description.—Body moderately robust (Fig. 8) and lacking tubercles. Carapace with patches of short setae on dorsum, as well as ventral and anterior to posterodorsal part of branchiocardiac carina; extremely long setae flanking base of, and between, teeth of postrostral carina.

Rostrum long, reaching as far as distal end of

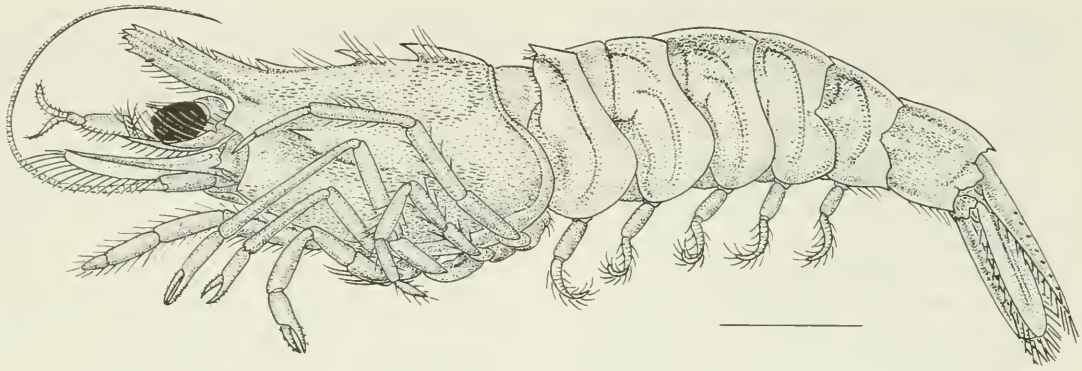


FIGURE 8.—*Sicyonia laevigata*, ♀ 9 mm cl, Punta Paitilla, Panama. Lateral view. Scale = 5 mm.

antennular peduncle, its length (0.40-0.77 cl) increasing linearly with carapace length (Fig. 9); relatively deep, usually with dorsal and ventral margins straight and subparallel; subhorizontal or upturned to as much as 35°; armed with two (25%), three (72%), or four (3%) dorsal teeth and two (5%), three (33%), or four (62%) apical teeth, additional rudimentary one present between two ventral ones; ventralmost tooth, largest of apical cluster, subterminal, directed anteriorly or curved upward, and distinctly removed from adjacent one. Position of first dorsal tooth ranging between 0.09 and 0.30 (mean 0.18) rl from level of orbital margin, and that of second tooth between 0.42 and 0.60 (mean 0.45) rl; third tooth, when present, between 0.76 rl and tip of rostrum (mean 0.87); and fourth, rarely present, located at tip. Two, occasionally one or three, minute but rather heavy movable spinules (often absent in adults) flanking ventral margin of rostrum, just posterior to apical teeth. Adrostral carina, subparallel to ventral margin of rostrum, extending to base of apical cluster.

Carapace with postrostral carina, barely distinct between teeth, bearing three unequal, acutely produced teeth: 1) epigastric tooth, situated between 0.06 and 0.16 (mean 0.12) cl from orbital margin, subequal to or only slightly larger than first rostral and conspicuously smaller than more posterior teeth; 2) middle tooth, placed between 0.35 and 0.50 (mean 0.45) cl from orbital margin; and 3) posterior tooth positioned between 0.68 and 0.80 (mean 0.72) cl from orbital margin, well in advance of posterior margin of carapace. Antennal spine absent or barely perceptible, antennal angle 90° to broadly obtuse, lacking buttress; hepatic spine long, sharply pointed, projecting from low buttress, and situated between 0.22 and 0.30 (mean 0.25) cl posterior to orbital margin. Postocular sulcus short; hepatic sulcus shallow, subhorizontal; hepatic carina lacking; branchiocardiac carina barely evident.

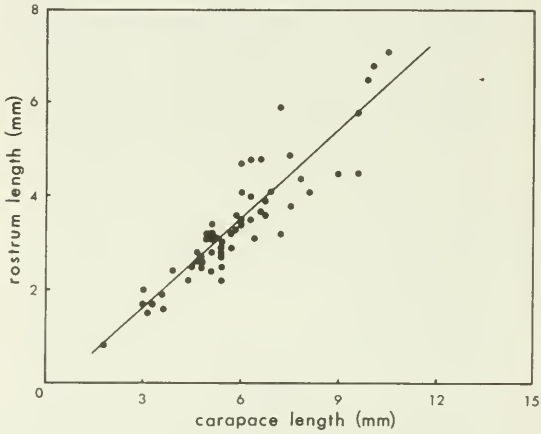


FIGURE 9.—*Sicyonia laevigata*. Relationship between rostrum length and carapace length (regression equation, $y = -0.39153 + 0.64127x$).

Ocular calathus broad and bearing conspicuous tuft of setae on dorsolateral extremity; ratio of length of lateral margin to width (across base of cornea) 0.54-0.65 (mean 0.60) and ratio length of lateral margin to cl 0.11-0.15 (mean 0.13).

Antennular peduncle with stylocerite produced in acute spine reaching 0.65-0.75 of distance between lateral base of first antennular article and mesial base of distolateral spine; latter extending only to about proximal 0.40 of second antennular article. Antennular flagella short, mesial one, about 0.7 as long as lateral; latter, about 0.4 cl.

Scaphocerite almost reaching or slightly sur-

passing distal end of third antennular article; lateral rib produced in long, slender spine slightly overreaching lamella. Antennal flagellum as much as 3 times as long as carapace.

Third maxilliped much stouter than pereopods. Basis and ischium of first pereopod armed with short but well-developed sharp spine projecting from distomesial margin.

Abdomen with dorsomedian carina low anteriorly, increasing in height posteriorly; carina on first somite produced in rather small, anteriorly directed tooth, smaller than posterior tooth on carapace; carina on second somite conspicuously incised (just dorsal to juncture of tergal sulci) and that on sixth terminating in short, sharp tooth.

Anteroventral extremity of pleuron of first three somites rounded; pleuron of fourth with posteroventral extremity angular or subangular, always unarmed; posteroventral extremity of fifth and sixth somites produced in very small, caudally directed, sharp tooth.

First somite with short anteromedian pleural sulcus (usually well marked but sometimes obscure dorsally, obsolete, or represented by shallow depression ventrally) and long, united posterior tergal-posteromedian pleural sulci. Second and third somites marked by 1) long anterior tergal (extending to base of pleuron) and short posterior tergal sulci; 2) anteromedian pleural sulcus, extending to near ventral margin on second somite but restricted to dorsal part on third, in both somites delimiting anterior shallow depression setting off weak prominence dorsally; and 3) posteromedian pleural sulcus, its dorsal extremity curving anteriorly ventral to (not joining) posterior tergal sulcus. Fourth and fifth somites with anterior tergal sulcus (that of fourth obliterated about midlength), merging with united posterior tergal-posteromedian pleural sulci. Sixth somite marked by weak, arched posteromedian pleural sulcus and bearing shallow longitudinal depression between low dorsolateral ridge and elongate cicatrix.

Telson with pair of short but strong fixed spines and two longitudinal rows of movable spinules on each side of median sulcus. Rami of uropod reaching or barely overreaching apex of telson.

Petasma (Fig. 10*A*, *B*) with rigid distal projection of dorsolateral lobule bulbous proximally, almost straight but with terminal part strongly curved dorsally; fleshy distal projection of ventrolateral lobule directed distolaterally, broad basally, and with slender but blunt terminal part curved proximally. Lateral margin of petasma

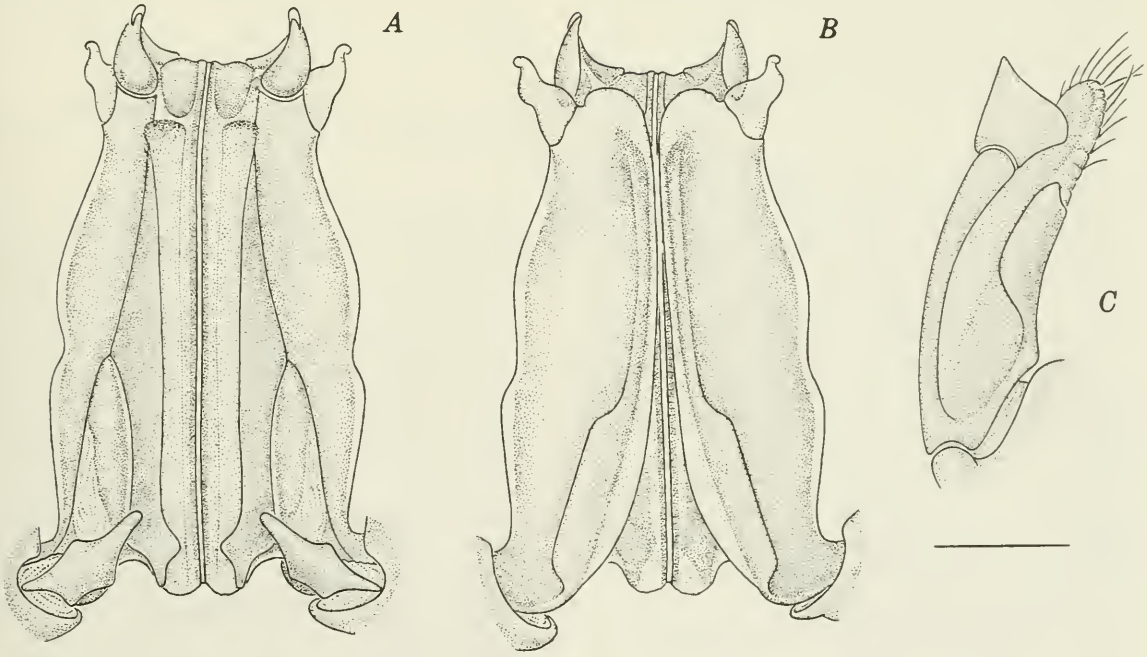


FIGURE 10.—*Sicyonia laevigata*, ♂ 5.7 mm cl, Isla Taboga, Panama. *A*, Petasma, dorsal view; *B*, ventral view; *C*, right appendix masculina, dorsolateral view. Scale = 0.5 mm.

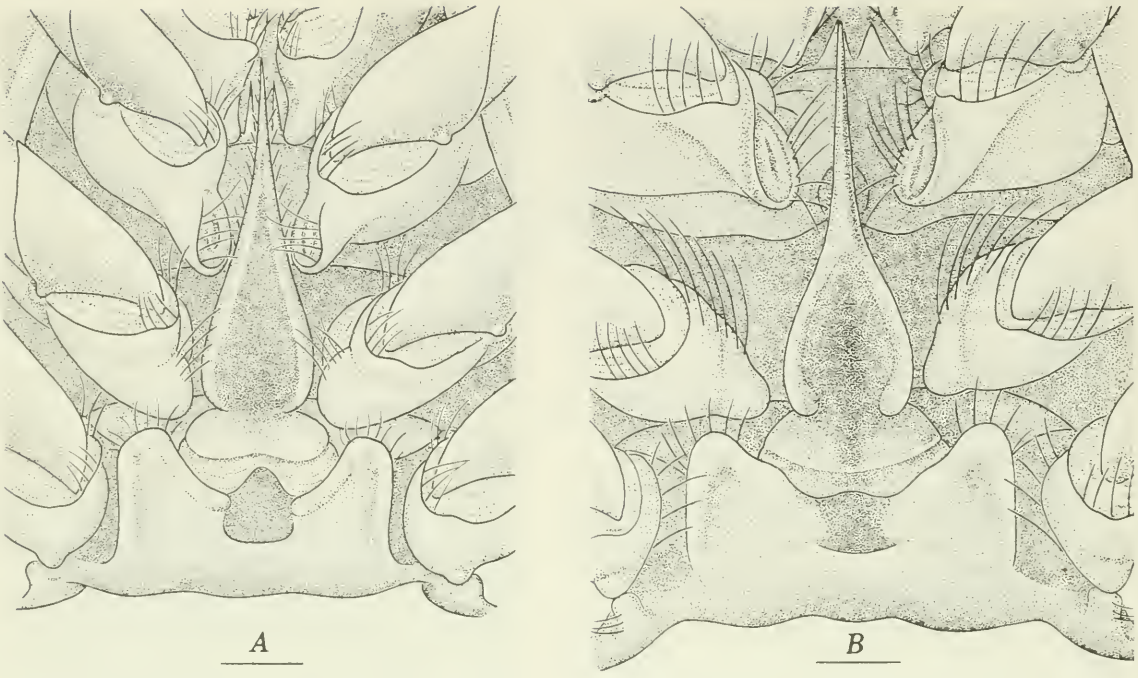


FIGURE 11.—*Sicyonia laevigata*. Thelyca. *A*, ♀ 7 mm cl, Isla San Lucas, Costa Rica; *B*, ♀ 9 mm cl, Punta Paitilla, Panama. Scales = 0.5 mm.

slightly to conspicuously notched near midlength.

Petasmal endopods coupled in males with carapace length as little as 2.9 mm, about 13 mm tl, petasma joined in all larger males.

Appendix masculina as illustrated in Figure 10*C*.

Thelycum (Fig. 11*A*, *B*) with plate of sternite XIV produced in elongate, subalate anterolateral lobules, their anteromesial borders strongly divergent; plate flat except for deep, broad, anteromedian depression, limited posteriorly by raised margin of posterior thoracic ridge. Median plate of sternite XIII narrow, lanceolate, tapering gently into sharp spine reaching as far as midlength of coxae of extended second pereopods; plate constricted and excavate at level of fourth pereopods; posterior component of plate with posterior margin entire to deeply emarginate and traversed by weak suture. Paired conspicuous spines projecting anteroventrally from posterior margin of sternite XI. Posterior thoracic ridge insensibly fused laterally with plate of sternite XIV.

The smallest impregnated female observed has a carapace length of 5 mm, about 18 mm tl.

Color.—Huff and Cobb (1979) presented a detailed account of the color pattern of this species based on specimens collected on Florida's west central shelf.

Maximum size.—Males 7.3 mm cl, about 34 mm tl; females 15 mm cl, about 53 mm tl.

Geographic and bathymetric ranges.—In the American Pacific, *S. laevigata* is known from Mazatlán (lat. 23°13′N, long. 106°25′W), Mexico (Rodríguez de la Cruz 1977); Isla San Lucas (9°56′N, 84°54′W), Golfo de Nicoya, Costa Rica; and the Golfo de Panamá, in the latter as far as Punta Paitilla (8°58′N, 79°31′W), Panama. In the western Atlantic this species ranges from off Cape Hatteras (35°08′30″N, 75°10′00″W), N.C., southward and into the Gulf of Mexico to northwest Florida, and off Yucatán. Also, it occurs through the Antilles and around the Caribbean coast of Mexico, Central America, and South America, and along the Atlantic coast of South America to Anse de Zimbros (27°13′S, 48°31′W), Santa Catarina, Brazil (Fig. 12).

In the Pacific, this shrimp has been taken from tide pools to a depth of 4-9 m, but in the Atlantic it occurs from the shore to as deep as 90 m. It occurs

on corals or other firm, rocky or shelly substrates, but occasionally, as reported by Wass (1955), on soft mud.

On the basis of their samplings and the observations made by Lyons et al. (1971), Huff and Cobb (1979) concluded that *S. laevigata* "shows some preference for grass habitats in estuarine and nearshore environments, associating with coarse substrates further offshore where seagrasses are absent."

This species has been found at salinities between 22 and 37‰ (Lyons et al. 1971 and Menzel 1956, respectively) and temperatures between 17° and 32°C (Lyons et al. 1971 and Camp et al. 1977, respectively).

Discussion.—*Sicyonia laevigata* is most similar to the Pacific *S. disparri* and the western Atlantic *S. parri*, but it may be readily distinguished from them by the following features. The epigastric tooth in *S. laevigata* is smaller than, instead of almost as large as, the other teeth on the postrostral carina. Also in *S. laevigata* this tooth is always situated anterior to the hepatic spine, between 0.06 and 0.16 (mean 0.12) cl from the orbital margin, whereas in *S. disparri* it is often located opposite or posterior to the hepatic spine but, if anterior, usually farther from the orbital margin, between 0.12 and 0.25 (mean 0.17) cl. The anteromedian pleural sulcus of the first abdominal somite in *S. laevigata* is short, commonly well defined (sometimes obscure) dorsally, but obsolete, cr represented by a shallow depression ventrally; in contrast, in *S. disparri* and *S. parri* it is long, extending to near the ventral margin of the pleuron, although sometimes it is interrupted dorsal to midlength. In *S. laevigata* the posterior pleural sulci are lacking, as they usually are in *S. disparri*, whereas in *S. parri* they are present. Furthermore, in the petasma of *S. laevigata* the distal projection of the dorsolateral lobule is directed distally, its tip curved dorsally, whereas in *S. disparri* and *S. parri* it is strongly curved mesially—but in the latter the tip is bent slightly dorsally. It should be pointed out that *S. parri*, like the other two species, lacks an antennal spine, possesses a spine on the basis and ischium of the first pereopod, and bears a dorsal incision on the dorsomedian carina of the second abdominal somite.

Remarks.—In 1980, I stated that the dorsal margin of the rostrum of *S. laevigata* is armed with three teeth, an opinion that was contrary to that of

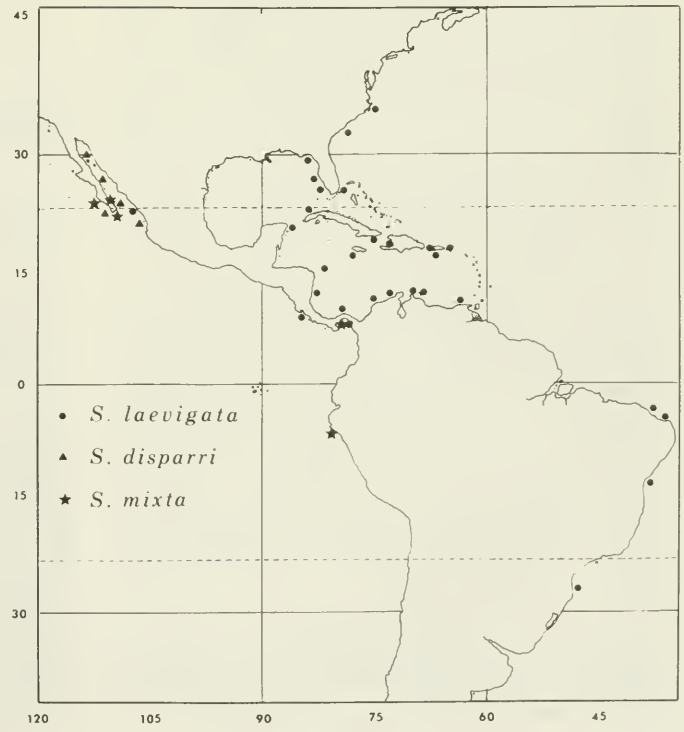


FIGURE 12.—Geographic distribution of *Sicyonia laevigata*, *S. disparri*, and *S. mixta*.

previous authors who noted that it bears only two; I was convinced at the time that they considered the variably situated third tooth, when located subterminally, an apical instead of a dorsal tooth. The study of the extensive collection available to me for the present project has indicated that this species sometimes (25% of the specimens) bears only two teeth, and occasionally four (3% of the individuals).

It should be mentioned that the holotype of this species was lost during the Chicago fire of 1871.

Material.—73 specimens from 41 lots.

Eastern Pacific—12 specimens from 6 lots.

Costa Rica—1♀, USNM, Isla San Lucas, 5 January 1930, M. Valerio.

Panama—1♂ 1♀, AHF, Isla Taboga, 4-9 m, 2 May 1939. 3♀, SIO, Isla Taboga, 3 m, 30 March 1967, R. Rosenblatt. 1♀, USNM, Punta Paitilla, intertidal, 1 July 1969, L. G. Abele and J. Graham. 1♀, USNM, Punta Paitilla, intertidal, 17 June 1969, J. Graham. 4♀, USNM, Punta Paitilla, 8 m, 13 April 1972, C. E. Dawson and party.

Western Atlantic—61 specimens from 34 lots.

United States—North Carolina: 1♀, USNM, off Cape Hatteras, 90 m, 17 October 1885, *Albatross* stn 2596. 2♀, USNM, off Morehead City, 14 July 1913, *Fish Hawk*. 3♀, USNM, Boque Sound (off Morehead City), August 1912, *Fish Hawk*. 1♀, USNM, Black Rocks (off New River), 13 m, 8 August 1949, A. S. Pearse. South Carolina: 1♀, USNM, mouth of Bulls Creek, 1891, *Fish Hawk*. 1♂, USNM, Charleston Harbor, 14.5 m, 13 March 1891, *Fish Hawk* stn 1659. 1♀, USNM, off S end of May River, Calibogue Sound, 18 m, 16 January 1891, *Fish Hawk* stn 1651. Florida: 1♀, USNM, Biscayne Bay, 7 July 1960, B. Petskin. 1♀, MCZ, off Key West, J. R. Miller. 1♂ 4♀, USNM, Marco, 2-5.5 m, H. Hemphill. 1♂, USNM, Punta Rassa, 2 m, February 1884, H. Hemphill. 1♀, USNM, Charlotte Harbor, March 1887, W. H. Dall. 2♂ 2♀, USNM, Sarasota Bay, H. Hemphill. 1♂, USNM, St Martin, 5.5 m, 15 January 1902, *Fish Hawk* stn 7222. 1♂ 3♀, USNM, off St Martin's Reef, 5 m, G. F. Moser. 2♂, USNM, off NW end St Martin's Reef, 1887, G. F. Moser. 1♀, USNM, Aucilla, 9 m, 6 November 1901, *Fish Hawk* stn 7148.

Cuba—1♂ 1♀, USNM, off Cayo Levisa, 4-5.5 m, 2 June 1914, *Tomás Barrera* Exped stn 14.

Jamaica—1♂, USNM, SE of Great Pedro Bluff, 27-29 m, 6 July 1970, *Pillsbury* stn 1223.

Haiti—1♀, AMNH, Port-au-Prince, W. Beebe.

Puerto Rico—2♀, USNM, Mayagüez, 23 m, 20 January 1899, *Fish Hawk* stn 6093. 1♂ 3♀, USNM, Mayagüez Harbor, 19-20 January 1899, *Fish Hawk*. 2♀, USNM, off Humacao, 23 m, *Fish Hawk*. 2♂ 2♀, USNM, off Isla Culebra, 27 m, 8 February 1899, *Fish Hawk* stn 6093.

Virgin Islands—St. Thomas: 1♀, USNM, 1884, *Albatross*.

Mexico—Quintana Roo: 1♂, USNM, off Isla Mujeres, 29.5 m, 11 June 1962, *Oregon* stn 3638. 1♂, USNM, SE of Isla Mujeres, 101-275 m, 9 September 1967, *Gerda* stn 880. 1♀, USNM, Bahía de la Ascensión, 17 April 1960, Smithsonian-Bredin Caribbean Exped stn 85-60.

Nicaragua—2♀, USNM, off NE Nicaragua, 55 m, 8 June 1964, *Oregon* stn 4930. 2♀, USNM, off Prinzapolca, 27 m, 28 January 1971, *Pillsbury* stn 1335. 1♀, USNM, E of Isla del Venado, 24 m, 28 January 1971, *Pillsbury* stn 1330. 1♂ 1♀, USNM, SE of Punta de Perlas, 27 m, 28 January 1981, *Pillsbury* stn 1334.

Colombia—1♀, USNM, Sabanilla, 1884, *Albatross*. 1♀, USNM, off Tucuracas, 9 m, 30 July 1968, *Pillsbury* stn 778.

Brazil—Santa Catarina: 1♀, MP, Anse de Zimbros, 5-0 m, 16 December 1961, *Calypso* stn 148.

Sicyonia disparri (Burkenroad 1934)

Figures 5, 12-17

Eusicyonia disparri Burkenroad 1934a:83, fig. 27 [holotype: ♀, YPM 4392, Bahía San Luis Gonzaga, Baja California Norte, Mexico, 17 May 1926, *Pawnee*]. Burkenroad 1938:80. Anderson and Lindner 1945:315.

Sicyonia disparri. Brusca 1980:256.

Vernacular names: rock shrimp (United States); camarón conchiduro, camarón de piedra, cacahuete (Mexico).

Diagnosis.—Antennal spine absent. Second abdominal somite with perpendicular incision on dorsomedian carina. First pereopod armed with short spine on basis and ischium. Postrostral carina bearing three subequal teeth, epigastric one as large, or almost as large, as posterior two teeth. Anteromedian sulcus of first abdominal somite clearly distinct to near ventral margin of pleuron; posteroventral extremity of fourth abdominal somite markedly angular. Petasma with distal projection of dorsolateral lobule curved me-

sially to apex. Thelycum with plate of sternite XIV produced in elongate anterolateral lobules, their anteromesial borders strongly divergent.

Description.—Body moderately robust (Fig. 13) and lacking tubercles. Carapace with short setae scattered over surface and extremely long ones between and flanking base of teeth on postrostral carina.

larger adults) flanking ventral margin of rostrum posterior to apical teeth. Adrostral carina, subparallel and distinctly dorsal to ventral margin, extending almost to base of apical cluster.

Carapace with weak postrostral carina bearing three subequal, acutely produced teeth: 1) epigastric tooth, often larger than first rostral and nearly as large as posterior teeth, situated between 0.12 and 0.25 (mean 0.17) cl from orbital

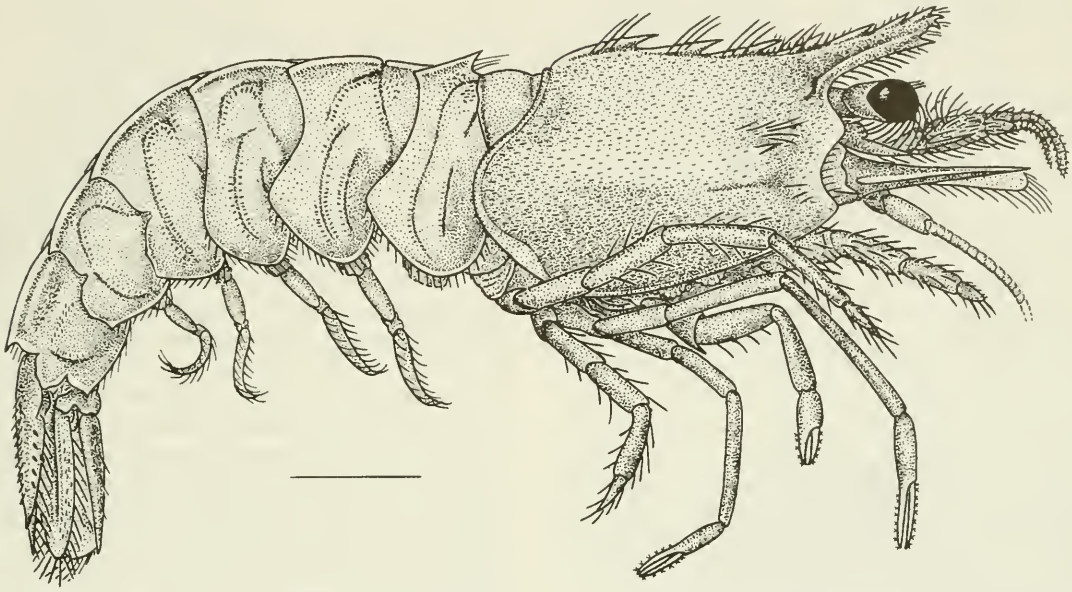


FIGURE 13.—*Sicyonia disparri*, holotype ♀ 10.4 mm cl, Bahía San Luis Gonzaga, Baja California Norte, Mexico. Lateral view. Scale = 5 mm.

Rostrum long, reaching as far as distal margin of second antennular article, its length (0.40-0.70 cl) increasing linearly with carapace length (Fig. 14); relatively deep, with dorsal and ventral margins subparallel; upturned to angle between 15° and 45°; armed with three dorsal teeth and two (7%), three (34%), four (57%), or five (2%) apical teeth, additional rudimentary one present between two ventral ones; ventralmost tooth largest of apical cluster, subterminal, directed anteriorly or curved upward, and distinctly removed from adjacent tooth. Position of first dorsal tooth ranging from slightly posterior to level of orbital margin, to as much as 0.30 (mean 0.18) rl anterior to it; that of second tooth between 0.40 and 0.65 (mean 0.50) rl from orbital margin, and that of third between 0.65 and 0.90 (mean 0.75) rl. Paired minute, movable spinules (sometimes absent in

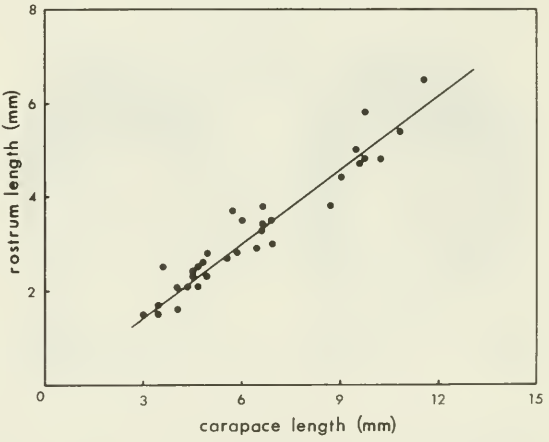


FIGURE 14.—*Sicyonia disparri*. Relationship between rostrum length and carapace length (regression equation, $y = -0.03809 + 0.51152x$).

margin, i.e., anterior, opposite, or posterior to hepatic spine; 2) middle tooth, largest of three, placed between 0.34 and 0.48 (mean 0.42) cl from orbital margin; and 3) posterior tooth, positioned well in advance of posterior margin of carapace, between 0.64 and 0.73 (mean 0.70) cl from orbital margin. Antennal spine absent, antennal angle broadly obtuse or rounded; hepatic spine long, sharply pointed, projecting from low buttress, and positioned between 0.20 and 0.30 (mean 0.25) cl posterior to orbital margin. Postocular sulcus short; hepatic sulcus shallow, subhorizontal; hepatic carina lacking; branchiocardiac carina at most barely evident.

Eye (Fig. 15*A*) with ocular calathus broad and bearing conspicuous tuft of setae on dorsolateral extremity; ratio of length of lateral margin to width (across base of cornea) 0.50-0.60 (mean 0.54) and ratio length of lateral margin to carapace length 0.08-0.13 (mean 0.11).

Antennular peduncle with stylocerite produced in acute spine reaching 0.65-0.85 of distance between lateral base of first antennular article and mesial base of distolateral spine; latter extending to proximal 0.45 of second antennular article. Antennular flagella short, mesial one about 0.8 as long as lateral; latter about 0.4 cl.

Scaphocerite reaching between midlength and distal end of third antennular article; lateral rib produced in long, slender spine conspicuously overreaching lamella. Antennal flagellum as much as 3 times as long as carapace.

Third maxilliped much stouter than pereopods. Basis and ischium of first pereopod each armed with well-developed sharp spine.

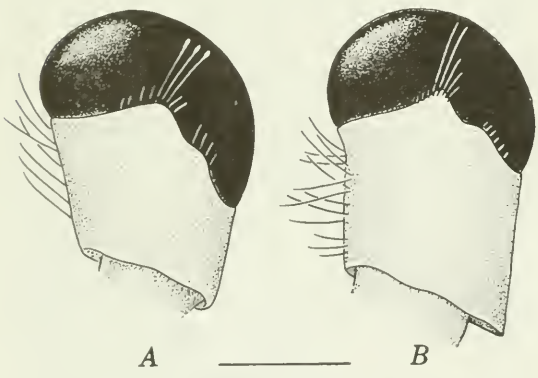


FIGURE 15.—Eyes. *A*, *Sicyonia disparri*, ♀ 9 mm cl, NW of Mantanchen, Nayarit, Mexico. *B*, *S. parri* (Burkenroad), ♀ 10.5 mm cl, east side of Cocoa Point, Barbuda. Dorsal views. Scale = 1 mm.

Abdomen with dorsomedian carina low anteriorly, increasing in height posteriorly; carina on first somite produced in rather small, anteriorly directed tooth, usually smaller than posterior tooth on carapace; carina on second somite conspicuously incised, and that on sixth terminating in short, sharp tooth.

Anteroventral extremity of pleura of first three somites rounded; pleuron of fourth with posteroventral margin straight to concave, its posteroventral extremity distinctly angular, occasionally armed with minute tooth; posteroventral extremity of fifth and sixth somites produced in very small, caudally directed, sharp tooth.

First somite traversed by long, sometimes interrupted, deep anteromedian pleural sulcus ending well above ventral margin without meeting long, united posterior tergal-posteromedian pleural sulci. Second and third somites marked by 1) long anterior tergal sulcus and relatively short posterior tergal sulcus; 2) anteromedian pleural sulcus, extending almost to ventral margin on second somite but restricted to dorsal part on third, in both somites delimiting anterior shallow depression setting off rounded prominence dorsally; and 3) posteromedian pleural sulcus, its dorsal extremity curving anteriorly, ventral to (not joining) posterior tergal sulcus. Fourth and fifth somites with anterior tergal sulcus (that of fourth usually obliterated at about midlength) fused with united posterior tergal-posteromedian pleural sulci. Sixth somite marked by strongly arched posteromedian pleural sulcus and bearing shallow, longitudinal depression between dorsolateral ridge and elongate, often ill-defined cicatrix.

Telson with pair of short but well-developed fixed spines and two longitudinal rows of movable spinules on either side of densely setose median sulcus—mesial row extending almost to base of spine. Both rami of uropod almost reaching or barely overreaching apex of telson.

Petasma (Figs. 5, 16*A*, *B*) with cornified distal projection of dorsolateral lobule bulbous proximodorsally, curved mesially, and minutely bifid distally; fleshy distal projection of ventrolateral lobule directed distolaterally, expanded basally and with slender but blunt terminal part slightly curved proximally. Lateral margin of petasma conspicuously notched just proximal to midlength, forming shoulder immediately proximal to notch.

Petasmal endopods coupled in males with carapace length as little as 3 mm (about 13 mm tl) but sometimes unjoined in individuals with

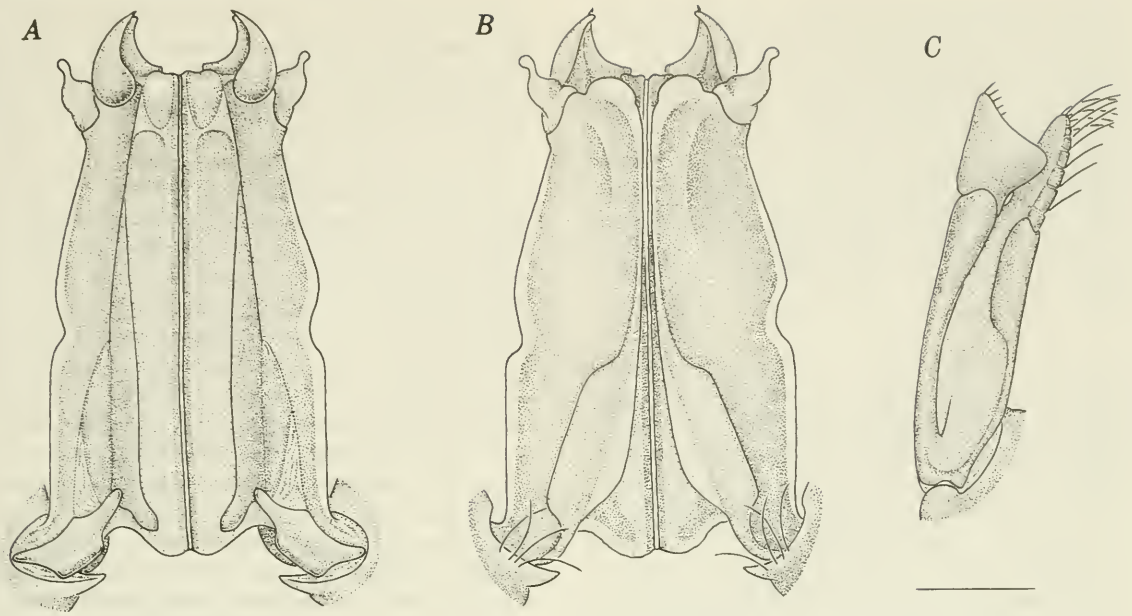


FIGURE 16.—*Sicyonia disparri*, ♂ 6 mm cl, Canal de San Lorenzo, Baja California Sur, Mexico. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scale = 0.5 mm.

carapace length as much as 4.9 mm (about 21 mm tl).

Appendix masculina as illustrated in Figure 16*C*.

Thelycum (Fig. 17) with plate of sternite XIV, produced in conspicuous anterolateral lobules, flat except for deep, broad, median depression. Median plate of sternite XIII narrow, lanceolate, tapering gently into long, sharp spine reaching as far as proximal 0.25 of basis of extended second pereopods; plate constricted and deeply excavate at level of coxae of fourth pereopods; posterior component of plate with shallow, broad posteromedian emargination and well-marked transverse suture. Paired conspicuous spines projecting anteromesially from posterior margin of sternite XI. Posterior thoracic ridge with sharp, concave anteromedian margin but areas immediately lateral to concavity flush with plate of sternite XIV.

The smallest impregnated female encountered has a carapace length of 5 mm, about 21 mm tl.

FIGURE 17.—*Sicyonia disparri*, holotype ♀ 10.4 mm cl, Bahía San Luis Gonzaga, Baja California Norte, Mexico. Thelycum. Scale = 1 mm.

Maximum size.—Males 6.9 mm cl, about 30 mm tl; females 11 mm cl, about 44 mm tl.

Geographic and bathymetric ranges.—In the Gulf of California, from Bahía San Luis Gonzaga (29°48′N, 114°22′W), Baja California Norte, and southward along the east coast of the peninsula, to Isla Santa Magdalena (24°55′N, 112°15′W), Islas Tres Marías, Nayarit, Mexico; also off Cabo San

Lucas (22°52′23″N, 109°53′23″W), Baja California Sur (Fig. 12). This species occurs at depths between 0.2 and 82 m, mostly at <24 m, and on sandy bottoms: sand, sand and shell, sand and gravel, and a mixture of sand mud, and coral. Among the eastern Pacific rock shrimps, *S. disparri* appears to have one of the most restricted distributions, being virtually confined to the Gulf of California and waters off Nayarit. Its presence south of the Gulf of California is reported here for the first time.

Discussion.—This shrimp is very similar to the geminate western Atlantic *S. parri* both in morphology and size. Burkenroad (1934a) first distinguished *S. disparri* by the absence of posterior pleural sulci on the anterior two abdominal somites and by the shorter, deeper, and more upturned rostrum. A few years later (1938), on the basis of three additional specimens, he pointed out other features in which *S. disparri* differed from his two specimens of *S. parri*: the shape of the posteroventral margin and extremity of the fourth abdominal somite, the presence of one or two pairs of movable spinules dorsal to the ventral margin of the rostrum near its anterior end, and the presence of four instead of three teeth on the dorsal margin of the rostrum. He stated that these characters are probably subject to variation and in so doing indicated that they might not be diagnostic. He noted, however, that the size and shape of the ocular calathus and the size and disposition of the cornea might prove to be diagnostic.

My examination of a relatively large collection of *S. disparri* has demonstrated that among the various features that Burkenroad (1934a, 1938) suggested to distinguish this species from *S. parri*, three are diagnostic: 1) the disposition of the rostrum, which is upturned between 15° and 45° in the former, is subhorizontal or inclined not more than 13° in the latter; 2) the shape of the posteroventral extremity of the pleuron of the fourth abdominal somite, which is angular in *S. disparri* and rounded in *S. parri*; and 3) the shape of the ocular calathus and the breath and disposition of the cornea. In the Pacific shrimp the calathus is broader than in the Atlantic species, the lateral margin ranges from 0.50 to 0.60 (mean 0.54) its width at the base of the cornea and the latter is obliquely disposed. In *S. parri* the lateral margin of the calathus (Fig. 15*B*) varies from 0.80 to 0.91 (mean 0.85) its width at the base of the cornea, and the latter is almost horizontally disposed. I have confirmed that the ratio of the lateral margin of the calathus to the length of the carapace is usually smaller in *S. disparri* than in *S. parri*, ranging from 0.08 to 0.13 (mean 0.11) in the former and from 0.13 to 0.17 (mean 0.13) in the latter, but sometimes overlapping.

The absence of posterior pleural sulci is a character that, although not infallible, serves almost always to separate *S. disparri* from *S. parri*, lacking in all specimens of the former except in two small individuals, in one of which traces of them are present in the first three somites, and in the other, in the second somite. In contrast, all individuals of *S. parri* bear such sulci. As Burkenroad anticipated, the shape of the posteroventral margin of the pleuron of the fourth somite, which is usually concave in *S. disparri* and convex in *S. parri*, is variable, sometimes straight in both shrimps.

The length of the rostrum is not a reliable diagnostic character, as previously suggested, only tending to be slightly longer in *S. disparri* than in *S. parri*—the ratio rl/cl ranges from 0.43 to 0.59 in the former and 0.36 to 0.55 in the latter. It does tend to be deeper, but not consistently, in the Pacific than in the Atlantic species.

Burkenroad (1938) also pointed out the presence of a fourth tooth on the dorsal margin of the rostrum in four of his specimens of *S. disparri*, but he considered this tooth to belong to the apical cluster (as I have in the meristic data presented here) when discussing differences in number of apical teeth between his smaller male and the remaining four shrimps. The number of apical teeth vary in both species; however, more tend to be present in *S. disparri*, 59% of the specimens possess more than three teeth (57% four, 2% five), whereas in *S. parri* 90% of them bear two or three (80% three, 10% two) and only 10% bear four teeth. In *S. disparri* the rostrum seems always to be armed with submarginal, movable spinules; their absence in a few adults is probably due to loss by accident. But among the specimens of *S. parri* I have examined, only one from south of João Pessoa, Paraiba, Brazil, bears a pair of such spinules. Another from Varadero, Cuba, possesses a single, very minute spinule located on the ventral margin of the rostrum, near the base of the ventralmost apical tooth.

The shape of the posteroventral margin of the pleuron of the fourth abdominal somite is variable, as Burkenroad predicted for *S. disparri*, sometimes straight in both species, but, as stated above, the posteroventral extremity is always angular in *S. disparri* and rounded in *S. parri*. In the

holotype of the former this extremity is sharply angular but unarmed, contrary to what was stated in the original description of the species; however, I have examined a few specimens in which the angle is produced in a small spine.

Sicyonia disparri is also quite similar to *S. laevigata* but the epigastric tooth is larger than that in the latter, usually almost as large as the other two teeth on the postrostral carina, and is located closer to the level of the hepatic spine, i.e., farther from the orbital margin, 0.12-0.25 (mean 0.17) cl from it rather than 0.6-0.16 (mean 0.12) cl. The anteromedian pleural sulcus of the first abdominal somite is always well defined in *S. disparri* whereas it is absent or, infrequently, rudimentary in *S. laevigata*; and the posteroventral extremity of the fourth abdominal somite in *S. disparri* is angular rather than rounded. Furthermore, whereas the distal projection of the dorsolateral lobule of the petasma is conspicuously curved mesially in *S. disparri*, it is directed distally and curved dorsally at its tip in *S. laevigata*.

The discussion of *S. parri* is based on 34 specimens, including the holotype (YPM 4395) and one male from the Bermudas, which represents the second record of the species from this area. Burkenroad (1938) reported it from the Bermudas, but his record has not been cited by subsequent authors, including me in my 1980 paper on the western Atlantic *Sicyonia*.

Material.—62 specimens from 20 lots.

Mexico—Baja California Norte: ♀, holotype, YPM 4392, Bahía San Luis Gonzaga, 17 May 1926, *Pawnee*. 1♀, paratype, YPM, Bahía San Luis Gonzaga, 17 May 1926, *Pawnee*. 1♀, AHF, off Isla Partida, 82 m, 8 March 1936. Baja California Sur: 1♂ 1♀, YPM, Bahía Santa Inés, 55 m, 11 April 1936, *Zaca* stn 142D-1. 6♂ 4♀, AHF, 1.6 km WSW of Punta Perico, Isla Carmen, 13-20 m, 21 March 1949, *Velero IV*. 1♂, AHF, Bahía Salinas, Isla Carmen, 13 m, 20 March 1940, *Velero IV*. 1♀, SIO, Bahía Salinas, Isla Carmen, 0.3 m, 13 July 1965, B. W. Walker. 1♀, CAS, Bahía Balandra, Isla Carmen, 22 May 1921, F. Baker. 1♂, AHF, Bahía Agua Verde, 18 m, 12 February 1940, *Velero III*. 6♂ 8♀, SIO, NW of Isla Santa Cruz, 0-3 m, 10 July 1960, B. W. Walker. 2♂ 2♀, SIO, Isla San José, 3-5 m, 29 March 1967. 1♂ 2♀, AHF, Canal de San Lorenzo, 11-24 m, 14 February 1940. 4♂ 9♀, USNM, off Isla del Espíritu Santo, 15 m, 30 April 1888, *Albatross* stn 2824. 2♀, SIO, off Punta Lobos, 18 m, 26 June 1961, R. Rosenblatt. 1♂ 1♀, USNM, Bahía La Ventana, 24-27 m, 20 April 1939, *Stranger* stn 38. 1♀, SIO, Ensenada de los Muertos, 9 m, 20 June 1961, R. Rosenblatt. 1♂, YPM, off Punta Arena, "Arena Bank," 64 m, *Zaca* stn 136D-30. 1♂, SIO, E of Cabo San Lucas, 0-6 m, 12 June 1961, R. Rosenblatt. Nayarit: 1♀, AHF, 1.6-3 km NW of Mantanchen, 21 December 1961. 1♀, AHF, Isla Santa Magdalena, Islas Tres Marías, 5.5-9 m, 9 May 1939.

Sicyonia mixta Burkenroad, 1946

Figures 12, 18-20

Sicyonia mixta Burkenroad, 1946:3, fig. 1-4 [holotype, ♂, NR (Stockholm) 2527; type-locality: "St. Joseph (probably San José, Lower California). Swedish Eugenie Expedition #818"]. Rodríguez de la Cruz, 1977:11.

Diagnosis.—Antennal spine well developed, projecting from short but strong buttress. First abdominal somite with dorsomedian carina uniquely lacking anterior tooth; second abdominal somite with anterior depression on dorsomedian carina limited posteriorly by subvertical wall. First pereopod with basis and ischium unarmed. Rostrum very short, not surpassing midlength of eye, bifid and bearing one dorsal tooth. Petasma with distal projection of dorsolateral lobule straight, but with tip curved dorsally; distal projection of ventrolateral lobule bifid, arms curved inwardly. Thelycum with plate of sternite XIV convex laterally and with deep median depression.

Description.—Body moderately robust (Fig. 18) and lacking tubercles. Carapace with long setae on dorsum, arc anterior to hepatic spine, and patch accompanying hepatic sulcus ventrally.

Rostrum very short, not surpassing midlength of eye, its length 0.13-0.16 cl; straight; armed with only one dorsal tooth situated almost at midlength of rostrum, and two minute apical teeth (tip bifid); ventral apical tooth located at same level or distinctly anterior to dorsal apical tooth. Conspicuous adrostral carina, close and subparallel to ventral margin, extending to base of ventral apical tooth.

Carapace with low postrostral carina ending markedly anterior to posterior margin of carapace and bearing three teeth: 1) epigastric tooth, smallest of three but larger than dorsal rostral tooth, placed well in advance of hepatic spine, between 0.05 and 0.08 cl from orbital margin; 2) middle tooth, as large as or slightly larger than posterior

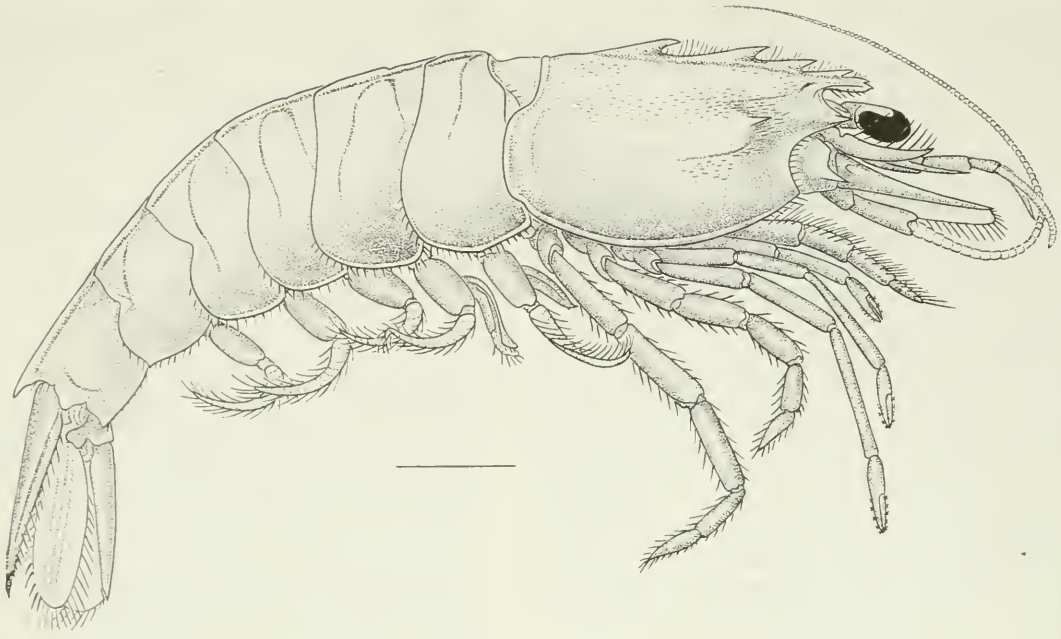


FIGURE 18.—*Sicyonia mixta* Burkenroad, 1946, ♂ 12 mm cl, off Cabo San Lucas, Baja California Sur, Mexico. Lateral view. Scale = 5 mm.

one, but about twice as high as anterior, situated posterior to hepatic spine, between 0.30 and 0.33 cl from orbital margin; and 3) posterior tooth, between 0.60 and 0.63 cl. Tuft of setae present at anterior base of each tooth. Antennal spine well developed, projecting from short buttress; hepatic spine long, sharp, borne on prominent buttress arising from swollen hepatic region; branchiocardiac carina barely distinct, only for short distance behind latter region. Postocular sulcus short and deep anteriorly, continuing posteriorly as well-defined groove; hepatic sulcus well marked, long, extending caudally to about level of apex of posterior tooth.

Antennular peduncle with stylocerite produced in long, acute spine, its length almost or quite equal to distance between lateral base of first antennular article and mesial base of distolateral spine; latter sharp, long, reaching as far as distal margin of second antennular article; flagella relatively elongate, mesial one about 0.20 cl, shorter than lateral, latter about 0.30 cl.

Scaphocerite reaching or surpassing antennular peduncle, sometimes by as much as 0.10 its own length; lateral rib produced distally in long, sharp spine overreaching lamella; antennal flagella incomplete in all specimens examined.

Third maxilliped stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with dorsomedian carina extending from first through sixth somites, carina weak on first and second, increasing progressively in height through sixth; carina on first somite lacking anterior tooth; on second interrupted by well-marked depression limited posteriorly by abrupt elevation, situated at level of juncture of tergal sulci; on fifth descending gradually instead of truncate posteriorly; and on sixth ending in large, acute, posterior tooth.

Pleuron of first abdominal somite with anteroventral margin slightly concave, anteroventral extremity rounded and unarmed; posteroventral extremity of first four somites also rounded, that of fifth usually bearing minute spine, and that of sixth always produced in small spine.

First somite with very short but deep anteromedian pleural sulcus and relatively weak (similar to most remaining sulci) but long posterior tergal (extending 0.60-0.66 height of somite). Second and third somites bearing short anterior and quite long posterior tergal sulci. Fourth somite with long posterior tergal sulcus, but anterior tergal almost indistinct. Fifth somite with barely distinct anterior tergal and relatively short posterior

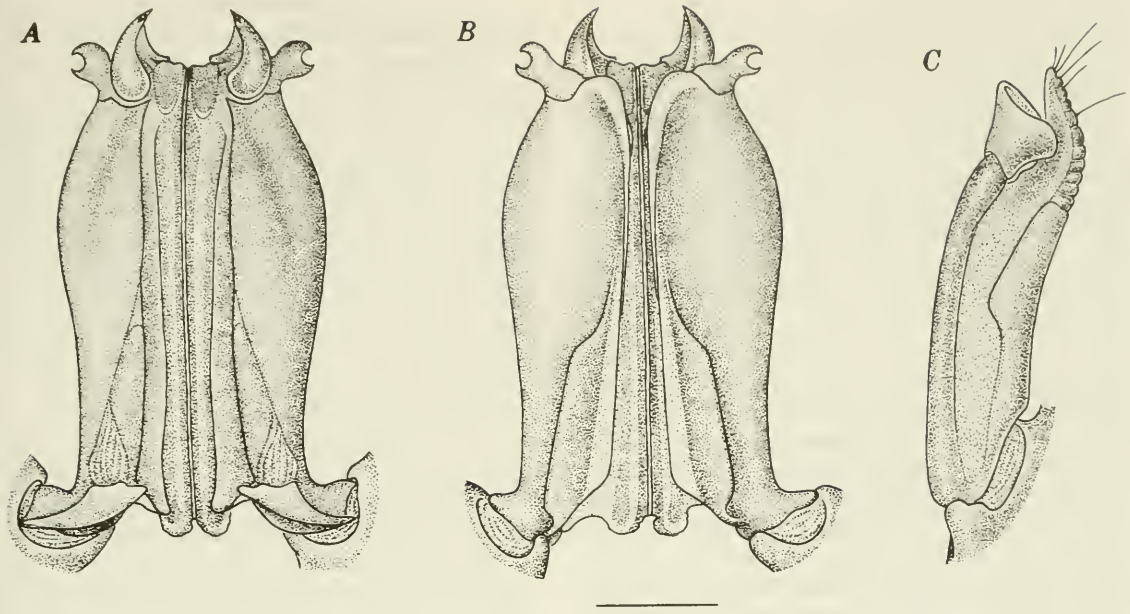


FIGURE 19.—*Sicyonia mixta*, ♂ 12 mm cl, off Cabo San Lucas, Baja California Sur, Mexico. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scale = 1 mm.

tergal, and sixth bearing weak anterior tergal and arched posteromedian pleural sulci.

Telson with paired fixed spines extremely minute (in the only specimen examined by me in which they are present). Rami of uropod, subequal in length, falling slightly short of apex of telson.

Petasma (Fig. 19*A*, *B*) with rigid distal projection of dorsolateral lobule bearing rounded proximodorsal prominence, extending almost straight distally but with tip curved dorsally. Distal projection of ventrolateral lobule bifid (arms curved), inclined laterally, and falling considerably short of adjacent projection.

Appendix masculina as illustrated in Figure 19*C*.

Thelycum (Fig. 20) with plate of sternite XIV, delimited by rounded lateral margins, raised in paired bulges sloping towards deep median depression. Median plate of sternite XIII roughly flaskshaped in outline, tapering into long, slender spine reaching proximal extremity of basis of anteriorly extended second pereopods; posterior component of plate with arched posterior borders flanking shallow to deep, broad median emargination, and traversed by strongly incised suture. Sternite XI armed posteriorly with paired, moderately long, acute spines. Posterior thoracic ridge with sharp, concave, anteromedian margin over-

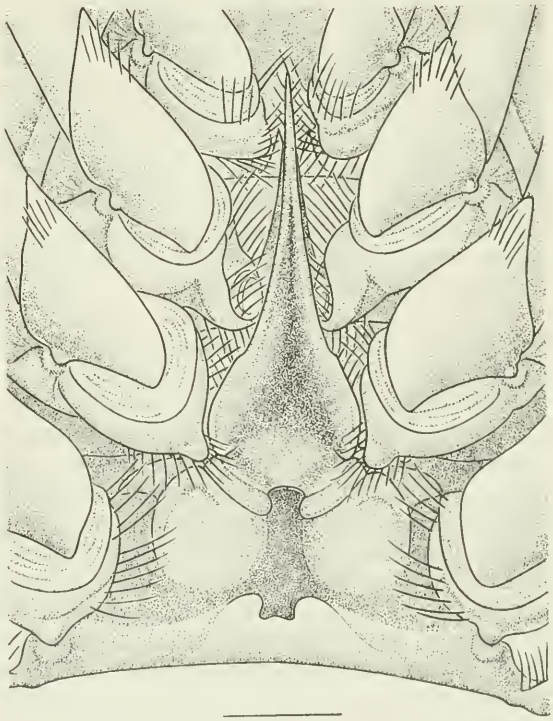


FIGURE 20.—*Sicyonia mixta*, ♀ 13 mm cl, off Isla Taboga, Golfo de Panamá, Panama. Thelycum. Scale = 1 mm.

lapping plate of sternite XIV but areas immediately lateral to it flush with preceding plate.

Color.—The specimen examined by me from Peru exhibits a dark colored mask in the shape of a "2" (the base situated anteriorly), disposed horizontally from the posterolateral part of the carapace onto the anterodorsal part of the first abdominal pleuron.

Maximum size.—Male 12.7 mm cl, about 43.5 mm tl; female 20 mm cl, 65.5 mm tl.

Geographic and bathymetric ranges.—In addition to the undetermined type-locality, "St. Joseph" (most probably San José, Baja California), it has been found in Bahía Almejas (24°29′18″N, 111°47′24″W) and off Cabo San Lucas, both on the ocean side of Baja California Sur, in Bahía de la Paz, on the eastern side of the latter, off Isla Taboga in the Golfo de Panamá, and off Puerto de Eten (6°22′S, 80°47′W), Peru (Fig. 12). *Sicyonia mixta* occupies shallow water at depths between 11 and 24 m.

The discovery of *S. mixta* first in the Golfo de Panamá and more recently northwest of Puerto de Eten, Peru, was surprising and represented a considerable extension of the range of the species. Previously, it was known only from the waters of Baja California, where the three male types were collected and where, in Bahía de la Paz, five females and a male were found (Rodríguez de la Cruz 1977). The specimen from off Puerto de Eten (a female 20 mm cl, 26.5 mm tl) was collected by M. Ñiquen from the RV *Humboldt* on 27 April 1983, and is deposited in the IMARPE.

Discussion.—As Burkenroad (1946) stated, *S. mixta* is unique in lacking a tooth on the anterior end of the dorsomedian carina of the first abdominal somite. Also this shrimp exhibits two of the basic characters of the species that Burkenroad (1934a) grouped in his Division II (the presence of a well-developed or clearly distinct antennal spine and the absence of basial and ischial spines on the first pereopod) at the same time that the dorsomedian carina of the second abdominal somite, although not incised, is abruptly depressed anteriorly. This depression seems to represent the deep incision or notch typical of the species of his Division I.

Among the American species (excluding those grouped in Division I), *S. mixta, S. disedwardsi, S. penicillata*, and two western Atlantic species —*S. typica* (Boeck 1864) and sometimes *S. olgae* Pérez Farfante, 1980—possess three dorsal teeth on the postrostral carina, two of which are situated posterior to the hepatic spine. In *S. mixta*, however, the posterior tooth arises on the postrostral carina considerably in advance of the posterior margin of the carapace, and the carina ends markedly anterior to the margin; in the other species the tooth arises nearer the margin where the carina ends. *Sicyonia mixta* also differs strikingly from the other four in the general sculpture of the abdomen; whereas in *S. mixta* it is not tuberculate and lacks all pleural sulci except the anteromedian on the first somite and the posteromedian on the sixth, in these congeners the abdomen is strongly tuberculate, exhibits deeper sulci, and possesses pleural sulci and all sixth somites. The bifurcate shape of the terminal part of the distal projection of the ventrolateral lobule of the petasma is another character that distinguishes *S. mixta* from the just mentioned relatives.

The relationships of this species are rather puzzling. Except for the distinctly depressed dorsomedian carina of the second abdominal somite, it does not share any other characters of importance with the species of Division I, represented by *S. disparri, S. laevigata,* and *S. parri*. Actually, it appears to be much closer to the group represented in the eastern Pacific by *S. disedwardsi* and *S. penicillata*, for in addition to possessing an antennal spine and lacking spines on the basis and ischium of the first pereopod, like them, it is armed with two teeth on the postrostral carina posterior to the hepatic spine. It seems to me that *S. mixta* has had, although remotely, a common origin with the above-mentioned group.

Remarks.—Because females of this shrimp have not been known previously, the above description of the thelycum is the first available for this species. In addition to the females cited from the Golfo de Panamá and off northern Peru, two other new records are presented here: one represented by a male from off Cabo San Lucas, Baja California Sur, and the other by a female from Bahía Almejas, Gulf of California. These four specimens, the types, and the six reported by Rodríguez de la Cruz (1977) are the only ones that have been recorded for this shrimp.

The holotype of this species and the paratype, in the Naturhistorisches Museum (Vienna), are the only extant types of the *Sicyonia* treated here that were not examined by me.

Material.—5 specimens from 5 lots.

Mexico—1♂ paratype, ZMB 6097, "California. Forrer" (?Ferrer). Baja California Sur: 1♂, SIO, Bahía Almejas, 11-24 m, 30 November 1961, F. H. Berry. 1♂, CAS, off Cabo San Lucas, 6 August 1932, *Zaca* stn D-21R.

Panama—1♀, USNM, off Isla Taboga, Golfo de Panamá, 10 March 1969, H. A. Clarke and A. Rodaniche.

Peru—1♀, IMARPE, off Puerto de Eten, 27 April 1983, M. Ñiquen, *Humboldt*, stn 8304, haul 175.

Sicyonia brevirostris Stimpson 1871

Figures 21-25

Sicyona cristata. de Saussure 1857:306. [Not *Hippolyte cristata* De Haan 1844:194 = *Sicyonia cristata* (De Haan 1844).]

Sicyonia brevirostris Stimpson 1871:132 [syntypes not extant; type-locality: S. Florida coast]. Kingsley 1878:69. Faxon 1896:162. De Man 1911:10. Pesta 1915:118. Hay and Shore 1918:380, pl. 25, fig. 4. Hedgpeth 1953:160. Hildebrand 1954:268, 1955:220. Menzel 1956: 41. Lunz 1957:4. Anderson 1958:1, fig. 5. Eldred 1959:5. Gunter and McCaughn 1959: 1194. Anderson 1962:1, fig. 15. Kutkuhn 1962:2. Chapa Saldaña 1964:4. Joyce 1965: 132. Cerame-Vivas and Gray 1966:263. Joyce 1968:254, unnumbered fig. Rouse 1969:136. Bayer et al. 1970:41. Zyznar 1970:87. Brusher et al. 1972:75. Cain 1972:79. Franks et al. 1972:54. Allen 1973:1. Cobb et al. 1973:7, fig. 3, 4A-C. Day et al. 1973:36. Bryan and Cody 1975:1. Brusher and Ogren 1976:158. Hooks et al. 1976:103. Kennedy et al. 1977:1. Pérez Farfante 1978: Sicyoniidae. Huff and Cobb 1979:51. Wenner and Boesch 1979:130. Holthuis 1980:58. Pérez Farfante 1980:772. Soto 1980a:68, 1980b:84. Castille and Lawrence 1981:519. Wenner and Read 1981:4. Arreguín Sánchez 1981:21. Pérez Farfante 1982: 370. Wenner and Read 1982:181. Williams 1984:43.

Eusicyonia edwardsi. Hay and Shore 1918, pl. 25, fig. 2. [Not *Sicyonia edwardsii* Miers 1881:367 = *Sicyonia typica* Boeck 1864.]

Eusicyonia brevirostris. Burkenroad 1934a:84, 1934b:117, 1939:57. Lunz 1945:4. Anderson et al. 1949:16. Anderson 1956:2. McConnell 1960:52.

Vernacular names: rock shrimp, hardback (United States); camarón de piedra, camarón conchiduro, camarón de roca (Mexico). FAO names (Holthuis, 1980): rock shrimp (English); camarón de piedra (Spanish); boucot ovetgernade (French).

Cobb et al. (1973) and Huff and Cobb (1979) presented extensive bibliographic references to this species, many of which are omitted from the above synonymy.

Diagnosis.—Antennal spine well developed and projecting from strong buttress. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing three teeth posterior to level of hepatic spine, rarely anterior one of these at level of or slightly anterior to hepatic spine. Rostrum armed with two dorsal teeth (rarely three). Petasma with distal projection of dorsolateral lobule relatively short, its apical part curved dorsally. Thelycum with plate of sternite XIV almost flat or slightly raised laterally in paired low bulges; posterior component traversed by well-marked suture. Branchiostegite lacking large spot or ocellus.

Description.—Body robust (Fig. 21). Carapace with dorsum covered by densely set, short setae; also patches of setae present anterior and ventral to hepatic spine, subjacent to hepatic sulcus and to branchiocardiac carina, and band of smaller setae on ventral part of branchiostegite. Patches also present on terga of abdominal somites. Abdomen heavily or moderately tuberculate, tubercles small, more numerous on first four somites.

Rostrum short, in young not overreaching distal end of second antennular article, in adults falling considerably short of distal margin of eye, its length increasing linearly with carapace length (Fig. 22), to about 16 mm cl, then growing little, rarely surpassing 6 mm (proportional length decreasing with increasing size from as much as 0.49 to as little as 0.15 cl); subhorizontal or upturned as much as 85°, tapering from base to tip, and armed with two (very rarely three) dorsal and two or three (four in one) apical teeth; latter subequal or ventral one extending farther anteriorly than dorsal and often upturned; when two teeth present, knob usually between them. Adrostral carina strong, bordering ventral margin and reaching end of rostrum.

Carapace with postrostral carina high, bearing

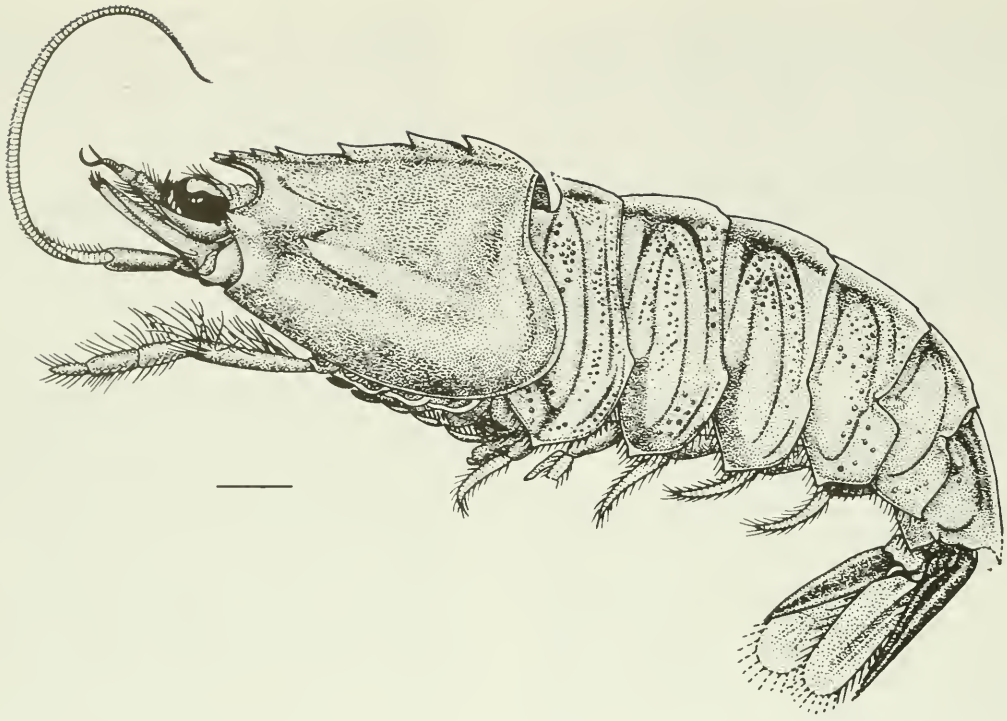


FIGURE 21.—*Sicyonia brevirostris* Stimpson, ♂ 18.1 mm cl, off Puerto Madero, Chiapas, Mexico. Lateral view. Scale = 5 mm.

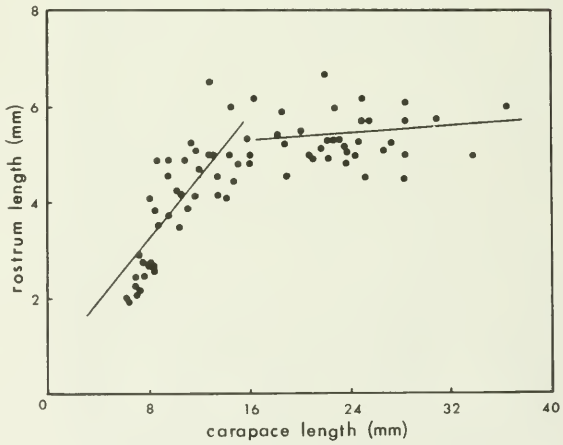


FIGURE 22.—*Sicyonia brevirostris*. Relationship between rostrum length and carapace length (regression equation for specimens with carapace length less than about 16 mm, $y = 0.52372 + 0.33342x$; regression equation for those larger, $y = 5.06145 + 0.01211x$).

four teeth: 1) epigastric tooth only slightly larger than first rostral, situated from anterior to orbital margin to as much as 0.1 cl posterior to it; and 2) three large teeth usually placed posterior to level of hepatic spine, anterior one (level with hepatic spine in only three specimens examined) smallest, situated between 0.20 and 0.28 (mean 0.25) cl from orbital margin, middle tooth between 0.52 and 0.60 (mean 0.55) cl, and posterior one between 0.74 and 0.79 (mean 0.75) cl. Antennal spine moderately long, projecting from strong buttress; hepatic spine, longer than antennal, acutely pointed and arising from moderately raised area between 0.20 and 0.25 (mean 0.23) cl from orbital margin.

Postocular sulcus with anterior part deep, continuing posteriorly as shallow groove; hepatic sulcus well marked; hepatic carina weak; branchiocardiac carina conspicuous, extending to or almost to transverse ridge near posterior margin of carapace.

Antennular peduncle with stylocerite produced in long, sharp spine, its length 0.85-0.90 distance between lateral base of first antennular article and mesial base of distolateral spine; latter extending as far as distal end of proximal 0.80 of second antennular article; antennular flagella short, mesial antennular flagellum shorter than lateral, 0.15-0.20 as long as carapace, lateral flagellum 0.19-0.23 as long.

Scaphocerite reaching or slightly overreaching distal margin of antennular peduncle; lateral rib ending distally in long, acute spine distinctly overreaching margin of lamella. Antennal flagellum about twice as long as carapace.

Third maxilliped stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with high dorsomedian carina extending from first through sixth somites: on first produced in strong anterior tooth, on fourth usually sloping posteriorly but sometimes abruptly truncate, and on fifth and sixth terminating in sharp tooth, latter longer.

Anterolateral margin of pleuron of first abdominal somite concave, anteroventral extremity of first through fourth somites ending in spine, that of first directed anterodorsally, those of second through fourth curved posterolaterally; posteroventral extremity of fourth through sixth somites bearing posteriorly directed, acute spine, that of fifth largest. Pleural spination of first four somites represented by tubercles in juveniles, becoming longer with increasing length of carapace.

First abdominal somite with long anteromedian pleural sulcus ending dorsally at anterior margin of tergum and converging with long posteromedian pleural sulcus ventrally; posterior tergal sulcus long or short, well marked or weak; posterior pleural sulcus well defined. Second and third somites with long anterior and posterior tergal sulci; anteromedian pleural sulcus continuous with anteroventral depression setting off prominence dorsally and ridge posteriorly; posterior pleural sulcus as on first somite. Fourth and fifth somites with anterior tergal joining curved, united posterior tergal-posteromedian pleural sulci dorsally; fourth also with shallow but clearly distinct caudodorsal depression, placed close to posterior margin. Sixth somite marked with faint anterior tergal and arched posteromedian pleural sulci, also bearing longitudinal ridge along base of dorsomedian carina and lateral depression (thickly covered with setae) dorsal to interrupted cicatrix. All sulci weak in juveniles, becoming deeper with age.

Telson with pair of short, often abraded, fixed subterminal spines. Rami of uropod subequal in length, reaching or slightly overreaching apex of telson.

Petasma (Fig. 23*A*, *B*) with rigid distal projection of dorsolateral lobule raised proximodorsally in rounded prominence, strongly curved dorsomesially, its distal part compressed, rounded ventrally, produced dorsally in short, subacute salient; mesial base of projection bearing short, dentiform prominence. Distal projection of ventrolateral lobule with firm terminal part curved laterally, convex dorsally, plane ventrally, and tapering to ventrally directed apex.

Petasmal endopods coupled in males as small as 6.3 mm cl, about 22 mm tl, but in individuals with as much as 13 mm cl, about 48 mm tl, they may not be joined.

Appendix masculina as illustrated in Figure 23*C*.

Thelycum (Fig. 24) with plate of sternite XIV produced in anterolateral lobules, almost flat or raised in paired low bulges sloping toward anteriorly deep median depression. Median plate of sternite XIII sagittiform, tapering gradually into long, slender spine reaching as far as proximal 0.25 of basis of extended second pereopods; plate strongly excavate and bearing shallow, lateral incisions at level of fourth pereopods; posterior component with deep, broad posteromedian emargination separating paired subtriangular processes limited anteriorly by well-marked transverse suture. Paired spines projecting anteroventrally from posterior margin of sternite XI, spines broad basally, often spiculiform apically. Posterior thoracic ridge narrow, with concave anteromedian margin well marked.

The smallest impregnated females encountered have a carapace length of 10 mm, about 44 mm tl.

Color.—The coloration of this shrimp was described in detail from live specimens from the Gulf of Mexico by Burkenroad (1939). Williams (1965) presented notes on the color of materials of North Carolina, and Cobb et al. (1973) recorded observations on individuals from the Yucatán shelf. In the latter, the dorsal part of the body is more reddish than in specimens from the northern Gulf of

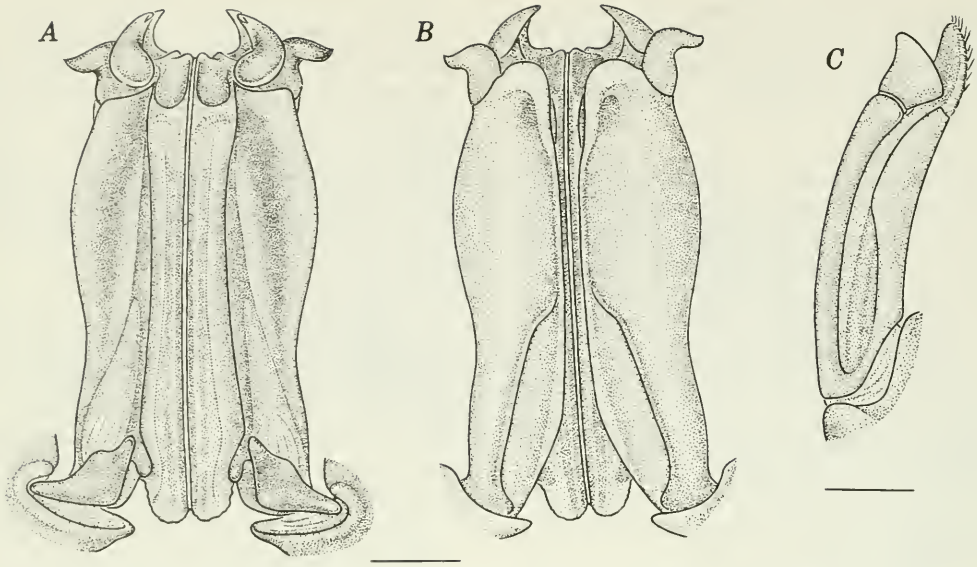


FIGURE 23.—*Sicyonia brevirostris*, 18.1 mm cl, off Puerto Madero, Chiapas, Mexico. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scales = 1 mm.

FIGURE 24.—*Sicyonia brevirostris*, ♀ 26.3 mm cl, off Cape Lookout, North Carolina, USA. Thelycum. Scale = 2 mm.

Mexico, which Burkenroad described as having the dorsum brown and the sides white, and also differs from shrimp occurring in North Carolina, in which the ground color is off-white.

Maximum size.—According to Holthuis (1980), 153 mm tl. Largest individuals examined by me: males 32 mm cl, about 125 mm tl; females 37 mm cl, about 130 mm tl. The only specimen from the Pacific, a male from off Puerto Madero, Chiapas, Mexico, measures 18.1 mm cl, 70 mm tl (latter from Burkenroad 1934a).

Geographic and bathymetric ranges.—In the eastern Pacific, off southern Mexico, from Colima (Chapa Saldaña 1964) to Chiapas (Fig. 25). In the western Atlantic, from Norfolk, Va., along the coast of the United States and the Bahamas to the southern coast of Cuba, and around the Gulf of Mexico from the Florida Keys to off Isla Contoy, Yucatán; perhaps also off Guyana (McConnell 1960). In the western Atlantic it occurs from shallow water to 329 m (Williams 1965), usually between 10 and 110 m, and rarely at depths >190 m. Exploitable populations are found between 34 and 55 m (Huff and Cobb 1979).

This species prefers sand and shell-sand substrates, but occasionally it is found on mud bottoms (Hildebrand 1954, 1955; Menzel 1956; Williams 1965; Cobb et al. 1973; Kennedy et al. 1977; Huff and Cobb 1979). The depths and substrates with which it was associated in the eastern Pacific were not recorded.

Discussion.—*Sicyonia brevirostris* is rather closely related to the western Atlantic *S. typica* and the eastern Pacific *S. disedwardsi*. It differs from both in possessing three, instead of two, large teeth on the postrostral carina posterior to the level of the hepatic spine and a caudodorsal depression on the fourth abdominal somite. It differs further from *S. disedwardsi* in 1) exhibiting well-marked posterior pleural sulci on the first three abdominal somites, which are lacking in the latter shrimp or, if present, weak, often distinct on only one or two somites; 2) having the distal projection of the dorsolateral lobule of the petasma turned dorsomesially, compressed distally, and produced apically in a short, subacute, dorsally directed salient—in contrast, in *S. disedwardsi* the projection is turned mesially and then dorsolaterally, its apical extremity produced in a relatively elongate, acutely pointed, laterally directed salient which often bears a crest; and 3) lacking an ocellus on the posterior part of the branchiostegite rather than bearing a large, brightly colored one such as that in *S. disedwardsi*.

Sicyonia brevirostris occupies water of high sa-

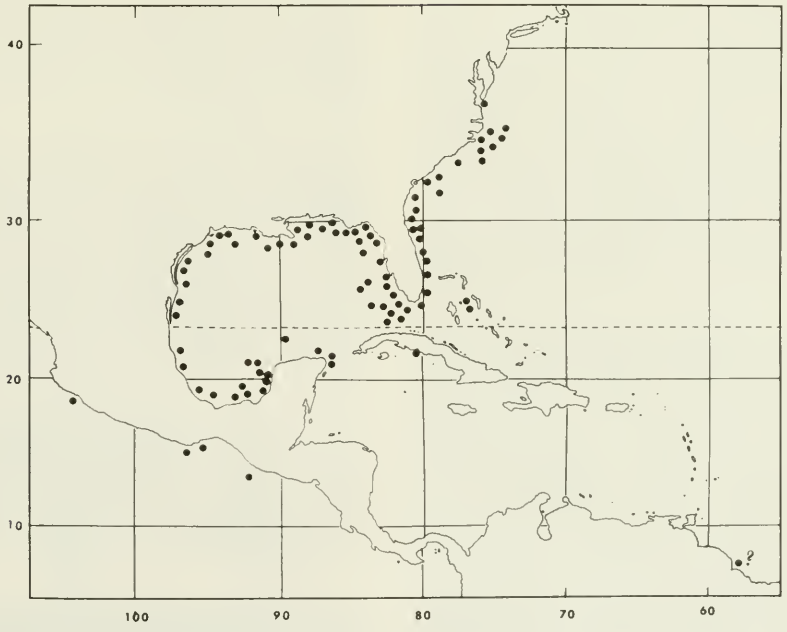


FIGURE 25.—Geographic distribution of *Sicyonia brevirostris*.

linity; recorded off east Florida and off west central Florida in salinities between 32.00 and 36.75‰ and 31.22 and 36.71‰ (Kennedy et al. 1977 and Huff and Cobb 1979, respectively) and off Mississippi between 27.8 and 34.6‰ (Franks et al. 1972). Only once, in the Chatham River, Fla., has it been recorded in an estuarine environment, at a salinity of 24‰ (Rouse 1969). The specimens on which this record is based consisted of larvae and small juveniles, and might have been misidentified, perhaps belonging to one of the other congeners found in that area. This shrimp, unlike other penaeoids, does not depend upon estuarine waters during its life cycle (Eldred 1959; Joyce 1965).

Many investigators (Lunz 1957; Joyce 1965; Brusher et al. 1972; Cobb et al. 1973; Brusher and Ogren 1976; Camp et al. 1977; Kennedy et al. 1977; Huff and Cobb 1979; Wenner and Read 1981) note that this species is predominantly nocturnal. Cobb et al. (1973) suggested that it burrows into the substratum during the day, thereby avoiding predation and capture by trawls.

Notes on biology and abundance.—Whereas the other American rock shrimps have been largely neglected, because of its considerable economic value, large size, and ready availability *S. brevirostris* has been the subject of a number of investigations. Cobb et al. (1973) and Kennedy et al. (1977) studied the reproductive cycle (including ovarian development in detail) of west central and east Florida populations, respectively. They concluded, as did Huff and Cobb (1979) who investigated the former population, that spawning and recruitment seem to occur throughout the year, with a peak of spawning from October to February off the west coast of Florida and during winter and early spring off the northeast coast. Cobb et al. (1973) suggested that a decrease in the daily photoperiod was responsible for the onset of spawning.

Morphometric studies by Kennedy et al. (1977) demonstrated that increase in total length occurs at the same rate in males as in females until they reach 20 mm cl, then the rate of increase of total length in females become less. They also found that the juveniles grow at an average rate of 2-3 mm cl per month whereas the adults grow at 0.5-0.6 mm cl. It was also estimated by them that the life span of this species is 20-22 mo. More recently Arreguín Sánchez (1981) presented biological fishery statistics (length/weight, growth, mortality, etc.) for this species.

Density of this shrimp in various populations fluctuates seasonally. Wenner and Read (1981, 1982) found that *S. brevirostris* is the dominant species of decapod crustacean on the continental shelf between Cape Fear, N.C., and Cape Canaveral, Fla., and that highest densities occurred in one summer of their 2½-yr study. Lunz (1957) noted a bimodal seasonal abundance off South Carolina, with peaks occurring from September through December and again in May. Kennedy et al. (1977) observed that peak abundance is reached during the fall in the east Florida population. In the Gulf of Mexico, off central Florida (Cobb et al. 1973; Huff and Cobb 1979), maximum abundance was found to exist from late summer through the fall. Off Apalachicola, Fla., (Allen 1973) highest densities seem to occur from June to October; in coastal water of Louisiana (on the basis of maximum production) and Texas (Brusher et al. 1972), from June through January, and in Bahía de Campeche (Hildebrand 1955) this species was more abundant in February than in July. It thus appears that throughout the range of this species maximum abundance occurs from summer through fall, and, in some areas, into early winter.

Kutkuhn (1962) calculated regression equations for predicting "headless" from "whole" weights and vice versa, and Cobb et al. (1973) presented equations for relating carapace length to total length for males and females, as well as others for carapace length and total weight for males and females, and for both sexes combined. Huff and Cobb (1979) also calculated the relationships of carapace length to total length and carapace length to weight for each sex.

Commercial importance.—Commercial fishing for *S. brevirostris* began in the United States in 1970 (Allen 1973) and since then production has increased noticeably, amounting to 3,351,000 lb, with a value of $3,222,000 in 1982 (Table 1). The fishing grounds are located off the southeast coast from North Carolina to central Florida (the most

TABLE 1.—Landings of *Sicyonia brevirostris* by areas and their values for 1982.[1]

Area	Pounds (heads-off)	Dollars
Georgia	369,000	353,000
East Florida	1,980,000	1,669,000
West Florida	1,001,000	999,000
Texas	1,000	1,000
Total	3,351,000	3,222,000

[1]Data provided by the Southeast Fisheries Center Statistical Survey Division, National Marine Fisheries Service, NOAA, Miami, Fla.

important ones by far being those off Cape Canaveral and Fort Pierce), and in the Gulf of Mexico off the coast of Florida (those off Apalachicola and Pensacola the most productive of the entire region) and western Texas. The production of the Carolinas was insignificant in 1982, last year for which landings are available.

This species is also exploited in Mexico off Isla Contoy, Quintana Roo, and in Bahía de Campeche. Arreguín Sánchez (1981) estimated that until 1978-79 the fishery off Isla Contoy, under optimal conditions, could have produced as much as 450 t (992,070 lb) of heads-on shrimp.

Remarks.—This species was first recorded from the eastern Pacific by Burkenroad (1934a). His record was based on a single specimen reportedly taken by the *Pawnee* off southern Mexico, in the Gulf of Tehuantepec, at lat. 14°40′20″N, long. 92°40′30″W. Later, Chapa Saldaña (1964) recorded five lots of this shrimp from the coast of Oaxaca, Golfo de Tehuantepec, which were in the collections of the Instituto Nacional de Investigaciones Biológico-Pesqueras, Mexico. Unfortunately, these specimens are no longer extant (Concepción Rodríguez de la Cruz[2]). Presence of S. brevirostris has not been confirmed by subsequent investigations in the region, including that of Sosa Hernández et al. (1980), who conducted a survey of the decapod crustaceans in the general area from which Burkenroad's and Chapa Saldaña's materials were obtained. Furthermore, representatives of the species were not found in the large collections of penaeoids from the Pacific coast of Mexico and Central America examined by me. Because of the large size of this shrimp (it may reach 153 mm), it should have been retained by the commercial shrimp trawls or other gear used off southern Mexico. The surprising fact that it has not been recorded from commercial catches since the appearance of Chapa Saldaña's report nor from collections resulting from exploratory work raises the possibility that the specimens cited above either bear incorrect data (as might be true of the correctly identified specimen examined by Burkenroad) or were misidentified.

McConnell (1960) reported this species from Guyana, but because it has not been recorded in studies (including my own) made of large collections of penaeoids obtained by research vessels and shrimp trawlers in the waters of that country or in any others south of Cuba, its presence there needs confirmation.

This is the only species for which full bibliographic references are not given. Because of its abundance, accessibility, and economic value, the literature on this shrimp is extensive. As stated above, much of it is cited in the works of Cobb et al. (1973) and Huff and Cobb (1979), consequently, I am including those references in which synonyms were created, articles not cited by them, others which appeared subsequent to their contributions, and all of those cited in the treatment below.

Material.—281 specimens from 66 lots.

Eastern Pacific—1 specimen.

Mexico—Chiapas: 1♂, YPM, off Puerto Madero, 9 April 1926, *Pawnee*.

Western Atlantic—280 specimens from 64 lots.

United States—North Carolina: 4♂ 2♀, USNM, off Rodanthe, 49 m, 20 October 1884, *Albatross* stn 2296. 14♂ 12♀, USNM, off Cape Hatteras, 64 m, 21 June 1957, *Combat* stn 396. 1♀, USNM, NE of Cape Hatteras, 55 m, 26 July 1969, *Oregon II* stn 10697. 3♂ 3♀, USNM, off Raleigh Bay, 26 m, 30 July 1969, *Oregon II* stn 10738. 2♂ 6♀, USNM, off Raleigh Bay, 33 m, 27 May 1962, *Silver Bay* stn 4028. 1♂, USNM, SE of Cape Lookout, 37 m, 12 March 1961, *Silver Bay* stn 2913. 3♀, USNM, off Cape Lookout, 43 m, 21 June 1957, *Combat* stn 397. 1♂ 3♀, USNM, Onslow Bay, 46 m, 2 August 1962, *Silver Bay* stn 4196. South Carolina: 2♂, USNM, off Port Royal Sound, 51-44 m, 25 June 1957, *Combat* stn 428. 1♂ 1♀, USNM, off Hilton Head Island, 40-46 m, 7 October 1957, *Combat* stn 514. 3♀, USNM, off Hilton Head Island, 64 m, 14 December 1961, *Silver Bay* stn 3657. Georgia: 3♂, USNM, off Cape Romain, 1941, J. Oney. 1♀, USNM, off Sapelo Island, 42 m, January 1940, *Pelican*. 4♀, USNM, NE of Savannah Beach, 40 m, 4 February 1940, *Pelican*. 6♂ 9♀, USNM, off Jekyll Island, 73 m, 15 March 1940, *Pelican*. Florida: 1♂ 2♀, USNM, NE of Fernandina, 31 m, 2 October 1951, *Combat* stn 505. 1♂ 2♀, USNM, off Fernandina, 42 m, 10 March 1976, *George M. Bowers* stn 37. 3♂ 3♀, USNM, off Ponte Vedra Beach, 24 m, 23 April 1956, *Pelican* stn 32. 4♂ 1♀, USNM, off St. Augustine, 329 m, 16 September 1956, *Combat* stn 119. 1♂, USNM, off Matanzas Inlet, 183 m, 18 November 1965, *Oregon* stn 5741. 13♂ 22♀,

[2]Concepción Rodríguez de la Cruz, Instituto National de Pesca, Secretaría de Pesca, México, D.F., Mexico, pers. commun., May 1983.

USNM, off Flagler Beach, 40 m, 7 November 1963, *Silver Bay* stn 5201. 2♂ 8♀, USNM, off Edgewater, 22 m, 1 December 1961, *Silver Bay* stn 3588. 1♂, USNM, off Cape Canaveral, 25 January 1962, *Silver Bay* stn 3704. 1♀, USNM, off Cape Canaveral, 70 m, 16 January 1966, *Oregon* stn 5860. 3♂, USNM, off Melbourne Beach, 40 m, 23 March 1956, *Pelican* stn 14. 5♂ 5♀, USNM, off Hutchinsons Island, 63 m, 11 November 1963, *Silver Bay* stn 5267. 2♂ 6♀, USNM, NE of St Lucie Inlet, 38-42 m, 21 May 1968, *Gerda* stn 1002. 2♂ 2♀, USNM, off Key Largo, 110-113 m, 26 January 1966, *Gerda* stn 769. 1♂, USNM, S of Islamorada, 49-40 m, 15 September 1965, *Gerda* stn 756. 2♂ 5♀, USNM, S of Pine Island, 170-194 m, 25 February 1969, *Gerda* stn 1023. 1♂ 2♀, USNM, S of Marathon, 57-69 m, 26 February 1969, *Gerda* stn 1030. 1♂ 1♀, USNM, NW of Marquesas Keys, 27 m, 28 May 1952, *Oregon* stn 562. 1♂ 3♀, USNM, SE of Dry Tortugas Islands, 59 m, 13 April 1965, *Gerda* stn 574. 1♂ 8♀, USNM, S of Dry Tortugas Islands, 68 m, 13 April 1954, *Oregon* stn 1004. 2♂ 6♀, USNM, S of Dry Tortugas Islands, 64 m, 12 April 1965, *Gerda* stn 566. 1♂, USNM, SW of Dry Tortugas Islands, 91 m, 8 March 1970, *Gerda* stn 1241. 1♂ 4♀, USNM, NW of Dry Tortugas Islands, 55 m, 18 June 1956, *Oregon* stn 1553. 1♂, W of Dry Tortugas Islands, 37 m, 7 March 1970, *Gerda* stn 1235. 1♂, USNM, off Appalachee Bay, 27 m, 9 March 1954, *Oregon* stn 905. 1♀, USNM, off St George Island, 37-35 m, 26 July 1957, *Silver Bay* stn 88. 2♀, USNM, off St George Island, 68 m, 10 March 1954, *Oregon* stn 916. 1♀, USNM, S of Apalachicola Bay, 64 m, 7 March 1954, *Oregon* stn 896. 1♂, USNM, off Grayton Beach, 43 m, 16 November 1952, *Oregon* stn 707. Alabama: 1♂, USNM, off Orange Beach, 37 m, 24 January 1957, *Oregon* stn 1651. 5♂ 4♀, USNM, off Dauphin Island, 70 m, 9 August 1950, *Oregon* stn 82. Louisiana: 1♂, USNM, off Beeton Sound, 40 m, 21 August 1962, *Oregon* stn 3713. 1♀, USNM, S of Mississippi Delta, 84 m, 12 September 1950, *Oregon* stn 101. 2♀, USNM, off Southwest Pass, Mississippi Delta, 60 m, 14 September 1980, *Oregon* stn 110. 1♂ 1♀, USNM, off Ship Shoal Lighthouse, 37-40 m, 12 September 1962, *Oregon* stn 3186. 1♀, USNM, off Pelican Island, 22 m, 8 March 1957, *Oregon* stn 1755. Texas: 6♂ 6♀, USNM, SE of Galveston, 20 m, 6 May 1938, *Pelican*. 5♀, USNM, S of Galveston, 18 m, 5 May 1938, *Pelican*. 6♀, SW of Galveston, 16 m, 5 May 1938, *Pelican*. 1♀, USNM, NE of Brownsville, 26 m, 5 February 1939, *Pelican*.

Mexico—Tabasco: 1♂ 1♀, USNM, off Paraíso, 35 m, 16 May 1954, *Oregon* stn 1057. 1♀, USNM, off Laguna Machona, 64 m, 16 May 1954, *Oregon* stn 1060. 1♀, USNM, NW of Punta Frontera, 60 m, 8 June 1970, *Oregon II* stn 10981. 3♂ 3♀, USNM, NW of Punta Frontera, 66 m, 9 June 1970, *Oregon II* stn 10982. Campeche: 2♂, USNM, N of Arrecifes Triángulos, 64 m, 17 August 1951, *Oregon* stn 411. 1♂, USNM, W of Cayos Arcas, 66 m, 16 June 1970, *Oregon II* stn 11005. 1♂, USNM, E of Cayos Arcas, 37 m, 11 December 1952, *Oregon* stn 720. 1♀, USNM, NE of Cayos Arcas, R. Ramírez and M. Flores, 48 m, 30 April 1959. 3♂ 1♀, USNM, NE of Cayos Arcas, 42 m, 10 December 1952, *Oregon* stn 719. 1♂ 2♀, USNM, 16 km, NE of Ciudad del Carmen, R. Ramírez and M. Flores, 29-37 m, 29 April 1959. 1♀, USNM, off Campeche, 13 m, 2 May 1959, R. Ramírez and M. Flores.

Sicyonia disedwardsi (Burkenroad 1934)

Figures 3, 7, 26-30

Eusicyonia disedwardsi Burkenroad 1934a:86, fig. 23, 29, 34 [holotype: ♂, YPM 4394; type-locality: Bahía Concepción, Baja California Sur, 3 May 1926, *Pawnee*]. Burkenroad 1938:82. Anderson and Lindner 1945:317. Castro 1966:17.

Sicyonia disedwardsi. Brusca 1973:219. Rosales Juárez 1976:41. Rodríguez de la Cruz 1977:11. Anonymous 1980:6. Brusca 1980: 256. Pérez Farfante 1982:371.

Vernacular names: rock shrimp, target shrimp, Japanese shrimp (United States); cacahuete, camarón de piedra, camarón de roca, camarón japonés (Mexico); camarón conchiduro (Mexico, Panama).

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing two teeth posterior to level of hepatic spine. Rostrum armed with two dorsal teeth. Petasma with distal projection of dorsolateral lobule short, stout, curved dorsomesially then laterally. Thelycum with plate of sternite XIV raised in relatively low, sometimes indistinct bulges; posterior component traversed by faint suture. Branchiostegite with large ocellus consisting of well-defined yellow center surrounded by purplish brown ring.

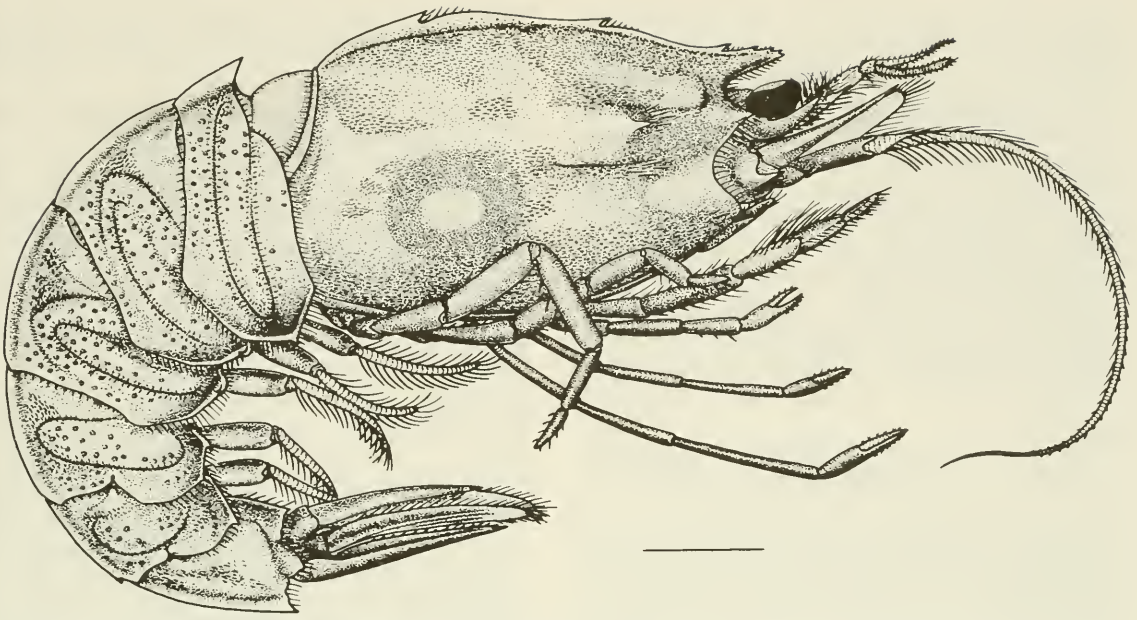


FIGURE 26.—*Sicyonia disedwardsi* (Burkenroad 1934), ♀ 34 mm cl, Golfo de Panamá, Panama. Lateral view. Scale = 10 mm.

Description.—Body robust (Fig. 26). Carapace studded with long setae anterior to hepatic spine and in pterygostomian region; patches of densely set shorter setae present on dorsum, in depression anterior to posterodorsal part of branchiocardiac carina, on branchiostegite, and subjacent to hepatic sulcus; patches also on tergum of abdominal somites and in depression just ventral to dorsal ridge of sixth somite. Abdomen bearing numerous tubercles on all somites (especially first three), except few or none on sixth.

Rostrum short, reaching distal margin of eye at most, its length increasing linearly with carapace length (Fig. 27) to about 20 mm cl, then growing little, not surpassing 6 mm (proportional length decreasing with increasing size from as much as 0.43 to as little as 0.13 cl); subhorizontal or upturned to as much as 45° (in young), tapering considerably from base to truncate, sometimes decurved tip; armed with two dorsal and two (96%) or three (4%) apical teeth. Adrostral carina, situated close to ventral margin, extending to end of rostrum.

Carapace with well-marked postrostral carina bearing three teeth: 1) epigastric small, only slightly larger than first rostral, situated from slightly anterior to orbital margin to 0.07 cl behind it; 2) middle tooth, larger than epigastric, placed well posterior to hepatic spine, between 0.29 and 0.38 (mean 0.33) cl from orbital margin; and 3) posterior tooth, larger than middle one, acutely pointed (usually abraded in larger adults), rising almost vertically before turning anteriorly or, more often, strongly inclined anteriorly, and situated between 0.68 and 0.80 (mean 0.72) cl from orbital margin; tuft of setae present at anterior base of all three teeth. Postrostral carina increas-

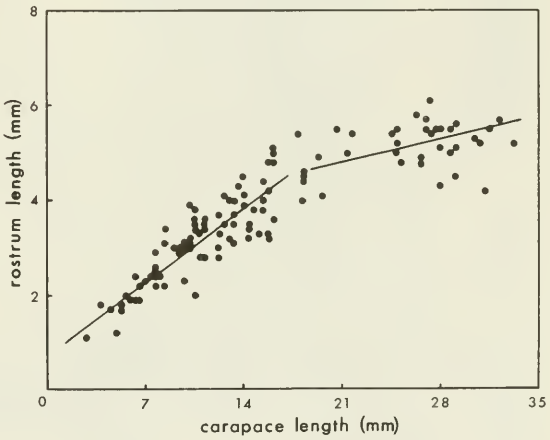


FIGURE 27.—*Sicyonia disedwardsi*. Relationship between rostrum length and carapace length (regression equation for specimens with about 20 mm cl or less, $y = 0.74318 + 0.21740x$; regression equation for those larger, $y = 3.81074 + 0.04939x$).

ing in height from low anterior part (between epigastric and middle teeth) to posterior tooth, descending gradually from it to posterior margin of carapace. Antennal spine relatively long, sharp, and projecting from short buttress; hepatic spine acutely pointed, arising from moderately raised area, and placed between 0.19 and 0.26 (mean 0.22) cl from orbital margin. Postocular sulcus short but deep, continuing posteriorly as barely distinct narrow groove; hepatic sulcus shallow; branchiocardiac carina broad, long, extending longitudinally from hepatic region almost to posterior margin of carapace where bifurcate: one branch curving dorsally and other, short, disposed ventrally.

Eye as illustrated in Figure 3. Ocular stylet with terminal part often bent laterally in young, but usually straight in larger individuals.

Antennular peduncle with stylocerite produced in long spine, its length 0.80 to 0.90 distance between lateral base of first antennular article and mesial base of distolateral spine; latter extending as far as distal 0.3 of second antennular article; antennular flagella short, maximum length 0.25-0.35 cl, mesial flagellum slightly shorter than lateral in young but subequal to or slightly longer in larger adults.

Scaphocerite nearly or quite overreaching antennular peduncle by as much as 0.15 its own length; lateral rib ending distally in long, acute spine conspicuously surpassing margin of lamella. Antennal flagellum as much as 2.2 times as long as carapace.

Third maxilliped stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with high dorsomedian carina extending from first through sixth somites, carina on first produced in strong tooth, sometimes disposed almost horizontally, but usually elevated as much as 55°, tooth tapering to sharp apex, and considerably larger than posterior one on carapace; carina on fifth somite produced in small tooth and that on sixth terminating in strong sharp one.

Anterior margin of pleuron of first abdominal somite straight or very slightly concave; anteroventral extremity of pleuron of first through fourth somites ending in spine, that of first usually directed anteroventrally, spines on second through fourth often curved posterolaterally; posteroventral margin of first through third somites rounded, that of fourth broadly angular, sometimes bearing node or minute spine, and that of fifth and sixth sharply angular and armed with small, caudally directed spine. Pleural spination of first four somites barely if at all distinct in juveniles, becoming stronger with increasing length of carapace.

First somite traversed by deep, long anteromedian pleural sulcus (sometimes obsolete along midlength), latter usually converging with united posterior tergal-posteromedian pleural sulci ven-

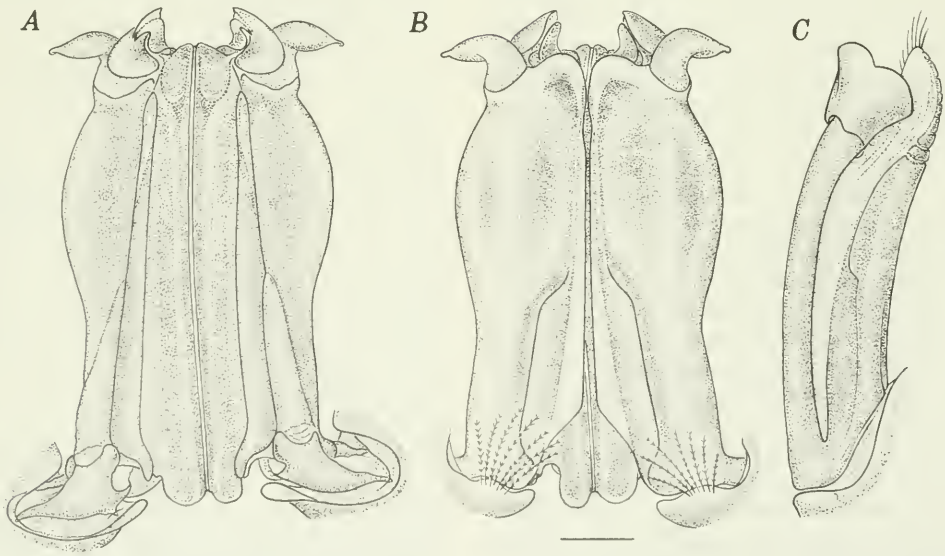


FIGURE 28.—*Sicyonia disedwardsi*, ♂ 23.5 mm cl, Golfo de Panamá, Panama. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scale = 1 mm.

trally, but its dorsal extremity often not reaching anterior margin. Second and third somites with anterior and often short posterior tergal sulci; anteromedian pleural sulcus frequently joining posteromedian pleural sulcus (sometimes obsolete) dorsally, and continuous with anteroventral depression setting off prominence dorsally and ridge posteriorly. Traces of posterior pleural sulcus occasionally present in one or more of first three somites. Fourth and fifth somites with anterior tergal joining curved, united posterior tergal-posteromedian pleural sulci. Sixth somite with shallow, arched posteromedian pleural sulcus; longitudinal ridge along base of dorsomedian carina delimited ventrally by weak depression lying dorsal to ill-defined cicatrix.

Telson with pair of small but clearly distinct fixed spines. Rami of uropod subequal in length and falling slightly short of or overreaching apex of telson by as much as 0.15 its own length.

Petasma (Fig. 28*A, B*) with rigid distal projection of dorsolateral lobule mesially inclined (instead of erect), strongly curved dorsomesially then laterally; distal part of projection slightly compressed, often bearing crest, rounded ventrally and produced laterally in elongate, acutely pointed salient. Distal projection of ventrolateral lobule with terminal part strongly curved laterally, bulbous dorsally, plane ventrally, with pointed tip curved proximoventrally.

Petasmal endopods coupled in males with carapace length as little as 5.5 mm (about 22.5 mm tl), but sometimes unjoined in individuals with carapace length as much as 10.5 mm (about 38.5 mm tl). These observations are similar to those noted by Burkenroad (1938).

Appendix masculina as illustrated in Figure 28*C*.

Thelycum (Fig. 29) with plate of sternite XIV raised in paired, low (sometimes indistinct), relatively short bulges, sloping toward deep, broad, median depression. Median plate of sternite XIII sagittiform, tapering gradually into long, slender spine reaching as far as proximal 0.25 of basis of extended second pereopods; plate deeply excavate and bearing arched lateral incisions at level of fourth pereopods; posterior component with deep, broad posteromedian emargination forming relatively elongate, posterolateral processes marked basally by rather faint transverse suture. Sternite XI armed posteriorly with pair of small, broad based spines. Posterior thoracic ridge either almost flush with plate of sternite XIV or with only anteromedian margin raised (ventrally).

Sperm receptacles as illustrated in Figure 7 (illustration based on specimen treated following method by Monod and Cals (1970)).

The smallest impregnated female encountered has a carapace of 12 mm, about 42 mm tl.

Color.—The only observation on color of fresh material from the Gulf of California (Anonymous 1980) indicates that the typical large spot found in the posterior part of the branchiostegite is purplish brown with a yellow center. The conspicuous ocellate spot persists in preserved specimens, appearing like a broad dark ring surrounding a light center.

Maximum size.—Male, 29.2 mm cl, about 102 mm tl; female 34 mm cl, about 108 mm tl.

Geographic and bathymetric ranges.—Southwest of Isla Santa Margarita (24°19′36″N, 111°46′24″W - 24°19′48″N, 111°47′06″W) to Bahía San Lucas,

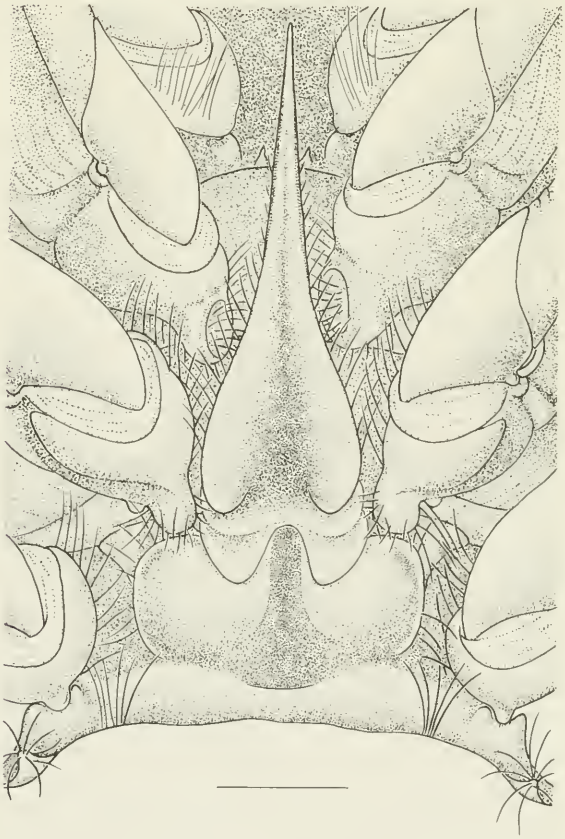


FIGURE 29.—*Sicyonia disedwardsi*, ♀ 21.3 mm cl, off Punta Gorda, Baja California Sur, Mexico. Thelycum. Scale = 2 mm.

Baja California Sur, in the Gulf of California along the central and southern parts of both coasts and southward to Bahía Chamela (19°33′42″N, 105°07′24″W), Jalisco, Mexico. Also from Bahía de Culebra (10°37′00″N, 85°40′00″W), Costa Rica, to northwest of Punta Caracoles (7°45′00″N, 78°24′30″W), Darién, Panama (Fig. 30). It has been found at depths between at least 18 (5-18) and 249 m, but seems to be most abundant at 30-60 m. It occurs on bottoms of shell, mud, fine sand, and rocks.

The occurrence of this shrimp along the west coast of Baja California Sur has not been previously reported.

Discussion.—*Sicyonia disedwardsi* is most similar to the western Atlantic *S. typica*. As stated above, among the American members of the genus lacking an incision or abrupt depression on the middorsal carina of the second abdominal somite, these two, together with *S. penicillata* and the western Atlantic *S. olgae* bear two relatively large teeth on the postrostral carina posterior to the level of the hepatic spine. The genitalia of *S. disedwardsi* and *S. typica* are so similar that they are almost indistinguishable, but in the petasma of *S. typica* the tip of the projection of the dorsolateral lobule is not so strongly produced and is usually directed dorsally rather than dorsolaterally. These two species, however, differ in the number and extension of abdominal sulci: in *S. typica* the first three somites exhibit well-marked posterior pleural sulci, which are absent or weak in *S. disedwardsi*, and the dorsal extremity of the united posterior tergal-posteromedian pleural sulci of the first somite reaches the anterior margin of the somite, whereas in *S. disedwardsi* the dorsal end usually does not reach the margin. Also in *S. typica*, the anteromedian pleural sulcus of the first somite is unbroken and that of the second joins the posteromedian, whereas in *S. disedwardsi* the former is often interrupted and the median sulci do not merge; in addition, the posterior tergal sulci of the second and third somites are much longer than in *S. disedwardsi*, in which they terminate considerably dorsal to the base of the respective pleuron. Furthermore, the rostrum of *S. disedwardsi* usually bears two teeth on the dorsal margin posterior to the apical teeth, whereas in *S. typica* it is often armed with only one.

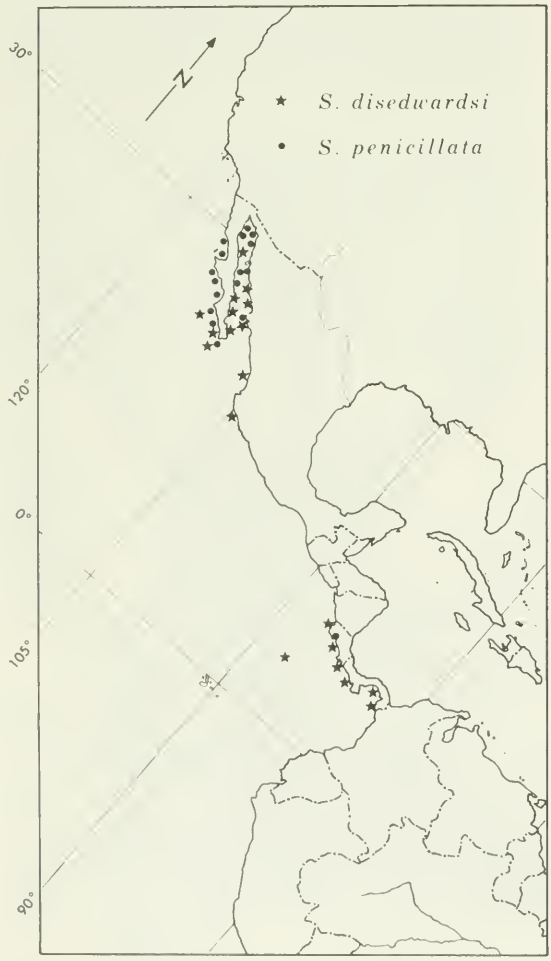


FIGURE 30.—Geographic distribution of *Sicyonia disedwardsi* and *S. penicillata*.

Sicyonia disedwardsi differs from *S. penicillata* by the same features of the abdomen that distinguish it from *S. typica*, except that in *S. penicillata* the posterior pleural sulci are more frequently present and slightly better marked than in *S. disedwardsi*. Too, the rostrum of *S. penicillata*, like that of *S. typica*, commonly bears only one dorsal tooth and is less elevated and usually shorter than in individuals of same size of *S. disedwardsi*. The two partly sympatric species can be separated readily by the genitalia. The unusually long distal projections of the dorsolateral and ventrolateral lobules in *S. penicillata* are not exhibited by any other of its congeners. Also, whereas in *S. disedwardsi* the thelycal plate of sternite XIV bears paired low (sometimes indistinct) bulges, in *S. penicillata* it is raised in strongly marked and more striking ones; the posterior component of the median plate of sternite XIII in *S. disedwardsi* exhibits a broad and deep posteromedian emar-

gination flanked by elongate processes and is traversed by a faint suture; in contrast, that of *S. penicillata* possesses a shallow emargination, often bearing a small anteromedian notch, and is traversed by a deep groove.

Long after they have been taken from the water, even after years in alcohol, specimens of this species may be readily recognized by a large ocellus, consisting of a well-defined yellow center surrounded by a broad purplish ring, on the branchiostegite. In *S. penicillata,* as in *S. typica*, the branchiostegite does not bear a large marking.

Burkenroad (1938) indicated that all members of *S. disedwardsi* may be distinguished from those of *S. penicillata* by the shape of the ocular stylets which in the former, according to him, diverge at the tip; they are straight in the latter. I have found, however, that although the stylets are laterally inclined distally in most of the young of *S. disedwardsi*, they are straight in some young and in many adults.

Commercial importance.—*Sicyonia disedwardsi*, one of the stubbiest of the rock shrimp occurring in the region, is usually taken with other penaeoids by the shrimp fleets operating in various areas from the Gulf of California to the Golfo de Panamá. Because of its size, it appears to have the potential of providing a fishery as has the similarly heavy *S. brevirostris* in the western Atlantic.

Material.—242 specimens from 54 lots.

Mexico—Baja California Sur: 6♂ 6♀, SIO, 3 km SW of Isla Santa Margarita, 48-57 m, 13 November 1964, *Black Douglas*. 5♂ 6♀, SIO, SW of Isla Santa Margarita, 29-40 m, 13 November 1964, *Black Douglas*. 2♂ 1♀, SIO, NW of Punta Márquez, 37 m, 4 December 1962, H. Perkins and R. Wisner. 12♂ 11♀, SIO, NW of Todos Santos, 38 m, 9 November 1964, *Black Douglas*. 3♂ 1♀, YPM, Bahía San Lucas, 15-29 m, 6 May 1936, *Zaca* stn 135 D-1. 1♀, YPM, Bahía San Lucas, 11-37 m, 6 May 1936, *Zaca* stn 135 D-9. 2♂ 2♀, YPM, off Punta Arena, 92 m, 30 April 1936, *Zaca* stn 136 D-24. 1♀, YPM, off Punta Arena, 82 m, 3 April 1936, *Zaca* stn 136 D-1. 4♂ 2♀, YPM, off Punta Arena, 64 m, 1 May 1936, *Zaca* stn 136 D-30. 3♂ 1♀, USNM, Bahía La Ventana, 24-27 m, 20 April 1939, *Strange* stn 38. 2♂1♀, SIO, off Punta Gorda, 81-84 m, 2 July 1965, C. Hubbs. 4♂ 3♀, USNM, Canal de San Lorenzo to Isla del Espíritu Santo, 4 April 1960, R. Mercado and G. Preciado. 2♂ 2♀, SIO, Bahía de la Paz, 55-79 m, 6 July 1965, R. Rosenblatt. 3♂ 9♀, SIO, Canal de San José, 64 m, 8 July 1965, R. Rosenblatt. 4♂ 10♀, SIO, Punta San Telmo, 10 July 1965, W. Baldwin. 8♂ 6♀, SIO, off W of Isla Monserrate, 92-73 m, 12 July 1965, R. Rosenblatt. 2♂, SIO, Bahía Concepción, 4 February 1940, D. Rouch. 1♂, holotype, YPM, Bahía Concepción, 3 May 1926, *Pawnee*. 2♂ 2♀, USNM, 4-6 m, off Punta Concepción, 12 April 1964, F. Rosales Juárez. 1♀, YPM, Bahía Santa Inés, 50 m, 13 April 1936, *Zaca* stn 143 D-1. 2♂ 1♀, YPM, Bahía Santa Inés, 37 m, 10 April 1936, *Zaca* stn 141 D-4. 1♀, YPM, Bahía Santa Inés, 13-16 m, 10 April 1936, *Zaca* stn 141 D-1. 2♂ 3♀, YPM, Bahía Santa Inés, 50 m, 11 April 1936, *Zaca* stn 142 D-1. 8♂, SIO, off Santa Rosalía, 35-26 m, 25 March 1960, R. Parker. 1♂, SIO, S arm of Bahía de los Angeles, 22-37 m, 26 April 1962, R. Rosenblatt. 2♂ 3♀, AHF, Puerto Refugio, Isla Angel de la Guarda, 38 m, 27 January 1940. Sonora: 1♂ 1♀, USNM, off Estero de Lobos, 47 m, 3 April 1978, Toral García. 1♀, USNM, 8 km off Guaymas, 26 m, April 1980, M. Hatziolos. 3♂ 5♀, INP, off Punta Rosa, 56 m, 2 April 1978, Toral García. 6♂ 4♀, USNM, SE of Punta Rosa, 54 m, 1 April 1978, Toral García. Sinaloa: 1♂, USNM, off San Ignacio, 25 May 1962, R. Bush M. 2♂, SIO, Isla de Altamura, 22-31 m, 26 May 1965, *El Golfo II* stn 50-6. 1♀, AHF, off Río San Lorenzo, 11-24 m, 14 February 1940. Nayarit: 1♂ 5♀, AHF, off Isla Isabela, 27-46 m, 9 May 1939. Jalisco: 1♂, SIO, Bahía Chamela, 27-18 m, 2 April 1973, *Agassiz*. Colima: 1♀, CAS, off Manzanillo, 17 July 1932, *Zaca*.

Costa Rica—1♂, AHF, Bahía de Culebra, 5-18 m, 24 February 1934. 2♀, AHF, S of Bahía de Culebra, 18 m, 25 February 1934. 1♀, SIO, Cabo Blanco, 60 m, 18 April 1973, *Agassiz*. 1♂, SIO, Cabo Blanco, 137-145 m, 19 April 1973, C. Hubbs and S. Luke. 1♀, UCR, near Cabo Blanco, 245 m, 28 April 1973, *Enriqueta*. 1♂, UCR, near Cabo Blanco, 249 m, 28 April 1973, *Enriqueta*. 1♂, UCR, near Puerto Quedos, 242 m, 26 April 1973, *Enriqueta*. 1♂, AHF, 5 km off Isla Manuelita, 146 m, 3 June 1973, *Velero IV*. 1♀, AHF, Golfo Dulce, 35-88 m, 26 March 1939, *Velero IV*.

Panama—2♂ 2♀, USNM, Golfo de Panamá, *Canopus* stn 670. 5♂ 11♀, USNM, Golfo de Panamá, *Canopus* stn 126. 2♂ 2♀, UP, Archipiélago de las Perlas, 11 December 1970, J. M. del Rosario. 1♂ 1♀, USNM, Isla San José, 64 m, 23 February 1973, fishermen. 3♂ 1♀, USNM, S of Isla del Rey, 44-42 m, 7 May 1967, *Pillsbury* stn 551. 1♀, AHF, Islas Secas, 46-48 m, 27 March 1939. 1♀, AHF, off Bahía Honda, 55-64 m, 1

March 1938. 5♂ 4♀, UP, between Punta Ave María and Ensenada Guayabo, 14 December 1969, staff Dep. Biol. Mar., UP. 3♂ 1♀, USNM, 12 km NW of Punta Caracoles, staff Dep. Biol. Mar., UP.

Sicyonia penicillata Lockington 1879

Figures 30-34

Sicyonia penicillata Lockington 1879:164 [syntypes (not extant): "Bolinas Bay (?Bahía de Ballenas), Lower California", 14 fm (fathom) (25.6 m); Angeles Bay (Bahía de los Angeles), Gulf of California, W. J. Fisher]. De Man 1911:112. Pesta 1915:118, fig. 7. Schmitt 1924:387. Brusca 1973:219. Rosales Juárez 1976:41. Rodríguez de la Cruz 1977:10. Anonymous 1980:7. Brusca 1980:256. Rodríguez de la Cruz 1981:1. Mathews 1981: 329.

Eusicyonia penicillata. Boone 1930:115 [part], pl. 36. Burkenroad 1934a:88, figs. 30, 31, 33, 1938:93. Steinbeck and Ricketts 1941:444. Castro 1966:17 [part]. Word and Charwat 1976:22, 2 figs.

Eusicyonia sp. Castro 1966:16, 17 [part], fig. 4.

Vernacular names: rock shrimp, target shrimp, Japanese shrimp (United States); cacahuete, camarón de piedra, camarón de roca, camarón japonés (Mexico). FAO names: peanut rock shrimp (English), camarón cacahuete (Spanish), boucot cacahouette (French).

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing two teeth posterior to level of hepatic spine. Rostrum armed with two dorsal teeth (rarely one). Petasma with distal projection of dorsolateral lobule acicular, long and slender. Thelycum with plate of sternite XIV raised in strong bulges; posterior component traversed by deep groove. Branchiostegite with moderately large purplish brown spot bearing poorly defined yellow center.

Description.—Body robust (Fig. 31). Carapace studded with long setae anteroventral to hepatic spine and pterygostomian region; patches of densely set shorter setae present on dorsum, in depression anterior to posterodorsal part of branchiocardiac carina, on branchiostegite and along hepatic sulcus; patches also on tergum of abdominal somites and in lateral depression of sixth somite. Abdomen with numerous tubercles on first three somites, fewer on last three.

Rostrum short, not surpassing distal margin of eye, its length increasing linearly with carapace length (Fig. 32) but proportionately longer in young (0.30-0.12 cl); usually straight but occasionally curved, subhorizontal or elevated as much as 45°; tapering, sometimes considerably, from base to truncate tip; and armed with one dorsal (rarely 2) and two (96%) or three (4%) apical teeth. Adros-

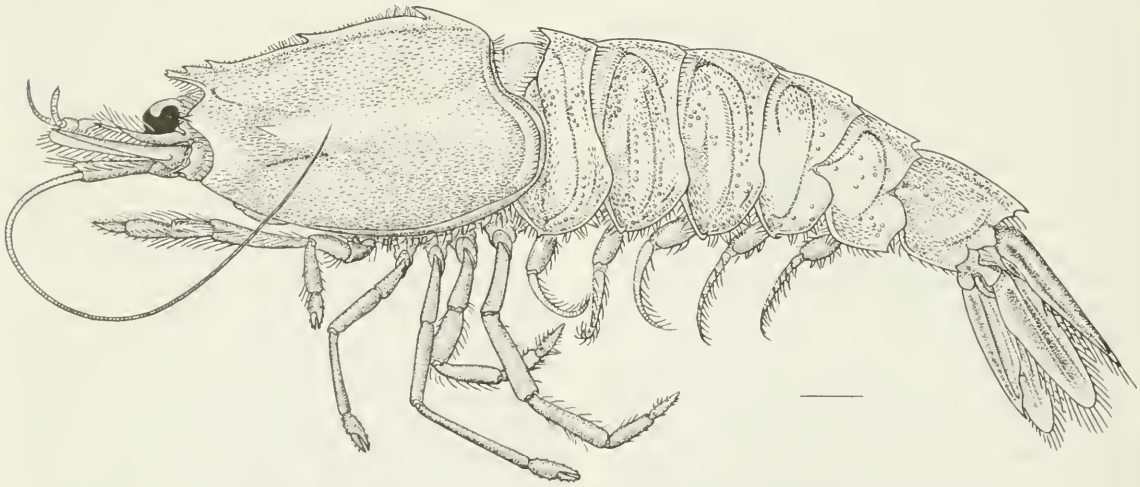


FIGURE 31.—*Sicyonia penicillata* Lockington, ♀ 23 mm cl, west of Punta Tasca, Isla Santa Margarita, Baja California Sur, Mexico. Lateral view. Scale = 5 mm.

tral carina, situated distinctly dorsal to ventral margin, strong and extending to end of rostrum.

Carapace with well-marked postrostral carina bearing three teeth: 1) epigastric tooth small, only slightly larger than first rostral, situated opposite (rarely) to <0.1 cl posterior to orbital margin; 2) middle tooth, larger than epigastric, sharp, placed well posterior to hepatic spine, between 0.33 and 0.40 (mean 0.36) cl from orbital margin; and 3) posterior tooth, larger than middle tooth, acutely pointed, rising almost vertically with only apical part inclined anteriorly or so inclined throughout, and situated between 0.70 and 0.77 (mean 0.74) cl from orbital margin; tuft of setae present at anterior base of all three teeth. Postrostral carina low anterior to middle tooth, high between middle and posterior one, and descending gradually from latter to posterior margin of carapace. Antennal spine relatively long, sharp, and projecting from short buttress; hepatic spine acutely pointed, larger than antennal, arising from moderately raised area between 0.20 and 0.26 (mean 0.22) cl from orbital margin. Postocular sulcus short but deep, continuing as shallow groove; hepatic sulcus well marked; branchiocardiac carina usually low (sometimes barely distinct) but occasionally quite prominent and long, extending to bifurcation near posterior margin of carapace, short branch curving dorsally and longer one ventrally.

Ocular stylet with terminal part straight or, occasionally, turned laterally.

Antennular peduncle with stylocerite produced in long spine nearly or quite reaching mesial base of distolateral spine; latter slender and sharp, extending as far as proximal 0.70 of second antennular article; antennular flagella short, with maximum length of 0.20-0.30 cl, in juveniles and young adults mesial flagellum slightly shorter than lateral one but in larger adults subequal to or slightly longer.

Scaphocerite reaching distal margin of antennular peduncle or overreaching it by no more than 0.10 of its own length; lateral rib ending distally in sharp spine distinctly surpassing margin of lamella. Antennal flagellum 2.4-2.7 times cl in young, and as much as 2.0 times in larger adults.

Third maxilliped stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with high dorsomedian carina extending from first through sixth somites, carina on first produced in strong, sharp, anterodorsally directed tooth, slightly to considerably larger than posterior tooth on carapace; carina on fifth somite produced in conspicuous tooth, and that on sixth terminating in strong acute one.

Anterior margin of pleuron of first abdominal somite almost straight; anteroventral extremity of pleuron of first through fourth somites ending in spine, that of first directed anteroventrally but that of second usually curved posterolaterally, resembling strong spines on third and fourth somites; posteroventral margin of first through third somites convex, on fourth broadly angular, and on fifth and sixth sharply so and armed with small caudally directed spine. Pleural spination of first four somites barely, if at all, distinct in juveniles, becoming stronger with increasing length of carapace.

First somite marked by long, anteromedian pleural sulcus converging with united posterior tergal-posteromedian pleural sulci ventrally, dorsal extremity of tergal reaching anterior margin of somite; posterior pleural sulcus weak, but usually clearly distinct. Second and third somites with anterior and posterior tergal sulci long, almost reaching base of pleuron; anteromedian pleural sulcus deep, continuous with anteroventral depression setting off elongate prominence dorsally and ridge posteriorly; posteromedian pleural sulcus also long, extending anterodorsally subparallel to posterior tergal sulcus; shallow posterior pleural sulcus commonly present in both somites. Fourth and fifth somites with anterior tergal and curved, united posterior tergal-posteromedian pleural sulci merging dorsally. Sixth somite marked by arched posteromedian pleural sulcus and bearing longitudinal ridge along base of dor-

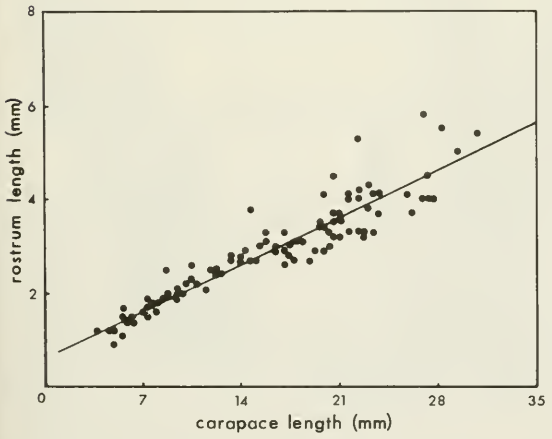


FIGURE 32.—*Sicyonia penicillata*. Relationship between rostrum length and carapace length (regression equation, $y = 0.65537 + 0.13963x$).

somedian carina delimited ventrally by depression lying just dorsal to well-defined cicatrix.

Telson with pair of small but well-developed fixed spines. Rami of uropod subequal in length and falling slightly short of or overreaching apex of telson by no more than 0.10 its own length.

Petasma (Fig. 33*A*, *B*) with short distal plate of dorsomedian lobule bearing distolaterally small, scalelike process bent inwardly (posteroventrally). Projection of distolateral lobule acicular, extremely long, about 0.75 as long as body of lobule, with heavily sclerotized triangular plate proximodorsally and flexible flagellum arising from ventrolateral surface; flagellum long, reaching between 0.60 and 0.75 length of projection from level of apex of triangular plate. Projection of ventrolateral lobule also long, about half length of acicular projection, bladelike and flexible, except for sclerotized tip curving proximally.

Petasmal endopods coupled in males with carapace length as little as 5.5 mm, about 22 mm tl, but sometimes unjoined in individuals with carapace length as much as 11 mm, about 39 mm tl.

Appendix masculina as illustrated in Figure 33*C*.

Thelycum (Fig. 34) with plate of sternite XIV raised in paired, well-marked, elongate bulges sloping toward deep, narrow, median depression. Median plate of sternite XIII lanceolate, tapering gradually into slender spine reaching as far as proximal 0.20 of basis of extended second pereopods; posterior component with relatively shallow posteromedian emargination (occasionally replaced by longitudinal incision) often forming small notch anteriorly, and flanked by short, rounded, posterolateral processes marked basally by deep transverse suture. Sternite XI armed posteriorly with pair of broad based, acute spines. Posterior thoracic ridge with anteromedian margin sharp and raised (ventrally), its lateral margins usually well marked, occasionally flush with plate of sternite XIV.

The smallest impregnated female encountered has a carapace length of 8.5 mm, about 33 mm tl.

Color.—Available information based on specimens that had been recently caught in the Gulf of California is limited to a purplish brown spot, with a yellow center not sharply defined, posteroventral to the hepatic spine; sometimes the entire spot is purplish brown (Anonymous 1980). Lock-

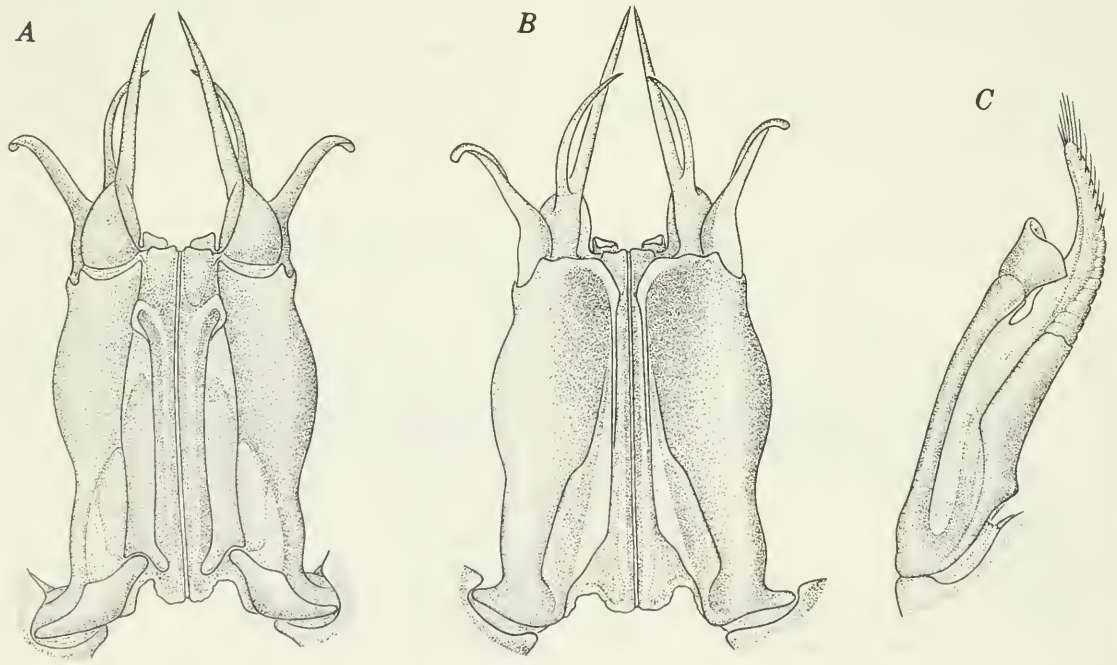


FIGURE 33.—*Sicyonia penicillata*, ♂ 21.5 mm cl, west of Punta Tasca, Isla Santa Margarita, Baja California Sur, Mexico. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scale = 1 mm.

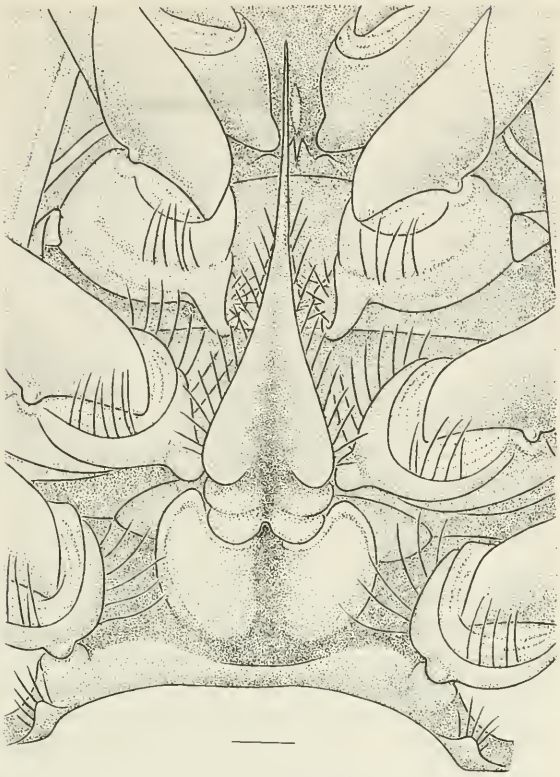


FIGURE 34.—*Sicyonia penicillata*, ♀ 23 mm cl, west of Punta Tasca, Isla Santa Margarita, Baja California Sur, Mexico. Thelycum. Scale = 1 mm.

ington (1879) noted that "Color after two weeks exposure to alcohol, bright red; with a dark red-brown ocellated spot on each side of the carapace. Antennae bluish." In many of the preserved specimens that I have studied, the ocellus appears as a dark circle.

Maximum size.—Males 32 mm cl, about 103 mm tl; females 35 mm cl, about 110 mm tl.

Geographic and bathymetric ranges.—From southwest of Punta Canoas (29°20′N, 115°02′W), Baja California Norte, Mexico (Fig. 30), southward to Bahía San Lucas, and in the Gulf of California, from the northern end to Bahía Concepción on the west and northern Sinaloa on the east; it seems to be absent from the southernmost part of the Gulf. It has also been found off Puntarenas (9°58′N, 84°50′W), Costa Rica (Boone 1930). This species occurs at depths between 0.60 and 180 m (latter by Boone 1930), mostly at 35-70 m. It has been recorded on sand (fine or coarse) and mud substrates that are sometimes densely covered with algae.

Discussion.—The closest affinities of *S. penicillata* seem to be with *S. disedwardsi* from which it differs most conspicuously in features of the petasma. The extremely long, slender, distal projections of both the dorsolateral (which bears a lateral flagellum) and ventrolateral lobules are far different from the short, stout, and simple projections of the petasma of *S. disedwardsi*, as well as from those of all other species of *Sicyonia*. These two species also exhibit significant thelycal differences. In the thelycum of *S. penicillata* the lateral bulges of the plate of sternite XIV are well defined; the posteromedian emargination of the median plate of sternite XIII is shallow (occasionally replaced by a longitudinal incision), often bears an anterior notch, and is flanked by short posterolateral processes marked basally by a conspicuous transverse groove. In the thelycum of *S. disedwardsi* the bulges are low, often indistinct, the posteromedian emargination of the median plate of sternite XIII is broad and deep, lacks a notch, and is flanked by relatively elongate posterolateral processes which are delimited anteriorly by a weak suture.

The following characters are also helpful but somewhat less reliable for distinguishing between the two species. In *S. penicillata* the rostrum is armed with only one tooth (rarely two) on the dorsal margin, instead of two as in *S. disedwardsi*; the stylocerite reaches the mesial base of the distolateral spine of the first antennular article, whereas in the latter species it often falls short of the base; the dorsal extremity of the united posterior tergal-posteromedian pleural sulci of the first abdominal somite reaches the anterior margin of the somite, whereas in *S. disedwardsi* often it does not; and the clearly defined although shallow posterior pleural sulci are usually present on the first three abdominal somites of *S. penicillata* but are quite weak or, more often, lacking on some or all of the latter.

Fresh material of this shrimp may be identified by a purplish brown spot on the branchiostegite, sometimes bearing a yellow center with diffuse border.

Burkenroad (1934a) presented a detailed discussion of the differences between *S. penicillata* and the western Atlantic *S. typica* (as *Sicyonia edwardsii* Miers, 1881). These species, which share among other characters three teeth on the postrostral carina and usually one dorsal and two api-

cal rostral teeth, differ strikingly in other features. In *S. typica* the sculpture of the abdomen is stronger than that in the eastern Pacific shrimp, exhibiting a long and deep posterior pleural sulcus on the first four somites instead of ones that are weak or even obsolete, and the telsonic spines are quite inconspicuous, rather than being well developed as they are in *S. penicillata*. Also, in *S. typica* the petasma lacks long slender distal projections as well as accessory flagella, the thelycal plate of sternite XIV is almost flat laterally instead of elevated in strong bosses, and the posteromedian emargination of the posterior component of the median plate is quite broad rather than narrow or even reduced to a longitudinal incision as it is in *S. penicillata*.

Remarks.—The types of this species were destroyed in the San Francisco earthquake and fire of April 1906 as were all of Lockington's types which had been deposited at the California Academy of Sciences (Dunn 1982). The locality of one of the syntypes, the one Lockington described in detail, "Bolinas Bay, Lower California," is uncertain. The NIS Gazetteer (Office of Geography, Department of the Interior, 1956) does not include any place or geographic feature under "Bolinas". On the west coast of Baja California Sur is Bahía de Ballenas or "Ballenas Bay" (NIS Gazetteer, p. 50), at 26°45′N, 113°26′W, and it is quite possible that the name of this locality was misspelled on the label accompanying the syntype or that Lockington misread and transcribed it as "Bolinas Bay". There is a bay by this name at 37°53′36″N, 122°39′54″W, in Marin County, California; however, I am inclined to think that Bahía de Ballenas actually is the place where the specimen was obtained because it is well within the range of the species, whereas Bolinas Bay is not only outside "Lower California" but also far beyond the known northern limit of this shrimp—southwest of Punta Canoas, Baja California Norte.

Commercial importance.—There is a fishery for rock shrimp in the northern half of the Gulf of California, and the catches are believed to consist largely of *S. penicillata* a very abundant species in that area. This fishery in 1979-80 produced 1,426,541 kg, but in 1981-82 (data recorded in Guaymas by the Instituto Nacional de Pesca, Mexico), the last year for which landings are available, the production declined sharply to 187,786 kg; fishing for rock shrimp is only seasonal, from February to June, with maximum catches being obtained during March and April (Concepción Rodríguez de la Cruz see footnote 2).

Material.—939 specimens from 56 lots.

Mexico—Baja California Norte: 2♀, SIO, SW of Punta Canoas (29°20′N, 115°02′W), 40 m, 6 September 1952, K. S. Norris. 1♂ 2♀, SIO, Bahía Playa María, 11 m, 1 April 1952, K. S. Norris. 3♀, SIO, Bahía Sebastián Vizcaíno, surface, 17 August 1952, *Spencer F. Baird*. 1♂, YPM, E of Isla Cedros, 1-73 m, *Zaca* stn 126D-3. 4♀, SIO, Bahía Sebastián Vizcaíno, 0-2 m, 14 August 1952, K. S. Norris. Baja California Sur: 3♂, SIO, Bahía Sebastián Vizcaíno, 55 m, 11 August 1952, K.S. Norris. 1♂, SIO, E of entrance to Laguna Ojo de Liebre, 2 m, 16 August 1952, K. S. Norris. 7♂ 5♀, SIO, Bahía Tórtolo, 31 March 1962, H. C. Perkins. 1♂ 2♀, SIO, E of Punta Asunción, Bahía Asunción, 15 m, 24 March 1951, R. Wisner and K. S. Norris. 6♂ 9♀, SIO, Bahía Asunción, 40-44 m, 17 November 1964, *Black Douglas*. 13♂ 11♀, SIO, Bahía Asunción, 68-64 m, 17 November 1964, *Black Douglas*. 11♂ 14♀, SIO, Laguna San Ignacio, 1.5 m, 11/12 February 1950, C. Hubbs. 3♂ 8♀, SIO, Bahía de Ballenas, 18 m, 14 February 1948, *Scripps*. 43♂ 50♀, SIO, SE of Punta Abreojos, 55-59 m, 17 November 1964, *Black Douglas*. 24♂ 22♀, SIO, W of Punta Pequeña, 37-40 m, 16 November 1964, *Black Douglas*. 26♂ 21♀, SIO, off Punta Pequeña, 55-51 m, 16 November 1964, *Black Douglas*. 4♂ 10♀, SIO, WSW of Punta Pequeña, 68-73 m, 16 November 1964, *Black Douglas*. 7♂ 5♀, SIO, NW of Santo Domingo del Pacífico, 45-40 m, 19 April 1969, D. Dockins. 26♂ 39♀, SIO, 15 km WSW of Boca de las Animas, 55-57 m, 16 November 1964, *Black Douglas*. 2♂ 3♀, SIO, S of Boca de las Animas, 137 m, 29 January 1964, C. Hubbs. 13♂ 7♀, SIO, between Boca de Santo Domingo and Boca de Soledad, 12 m, 5 February 1964, A. Stover and B. Zahuranec. 1♀, USNM, Boca de Soledad, 26 April 1964, H. Chapa. 1♀, SIO, channel N of Bahía Magdalena, 6 m, 30 January 1964, A. Stover and B. Zahuranec. 48♂ 44♀, SIO, NW of Isla Santa Magdalena, 73 m, 15 November 1964, *Black Douglas*. 3♂ 3♀, SIO, Bahía Santa María, 0-36 m, 8 December 1962, H. C. Perkins. 1♂ 1♀, SIO, Bahía Magdalena, 42-44 m, 29 November 1962, F. H. Berry. 1♀, USNM, Bahía Magdalena, surface, 10 July 1953. 14♂ 9♀, SIO, Bahía Magdalena, 37-40 m, 24 August 1960, F. H. Berry. 8♂ 6♀, YPM, Bahía Magdalena, 0.6-0.9 m, 1936, *Zaca* [unnumbered stn]. 1♀, AHF, Bahía Magdalena, between mainland and Punta Redonda, 15 m, 5

February 1974, *H. G. Moser* stn 13. 7♂, SIO, off Bahía Magdalena, 88 m, 3 February 1964, C. Hubbs. 5♂ 6♀, SIO, Bahía Almejas, 21-24 m, 11 November 1964, *Black Douglas*. 50♂ 50♀, SIO, SW of Isla Santa Margarita, 29-40 m, 13 November 1964, *Black Douglas*. 40♂ 40♀, SIO, 3 km SW of Isla Santa Margarita, 46-57 m, 13 November 1964, *Black Douglas*. 18♂ 8♀, SIO, SW of Isla Santa Margarita, 75-80.5 m, 13 November 1964, *Black Douglas*. 1♂ 5♀, SIO, SW of Isla Santa Margarita, 88-90 m, 13 November 1964, *Black Douglas*. 3♂ 2♀, SIO, W of Punta Tasca, Isla Santa Margarita, 7 July 1955, *Andrés* stn 143. 1♀, SIO, 11 km NW of Punta Márquez, 55 m, F. H. Berry. 2♀, SIO, 14.5 km WNM of Punta Márquez, 92 m, 4 December 1962, F. H. Berry. 1♂, YPM, Bahía San Lucas, 11-37 m, 6 May 1936, *Zaca* stn 135D-11, 12. 1♂, SIO, Bahía Santa Inés, 40-82 m, 14 July 1965, C. Hubbs. 34♂ 22♀, YPM, Bahía Concepción, 3 May 1926, *Pawnee*. 7♂ 2♀, SIO, off Santa Rosalía, 35-36 m, 25 March 1960, R. Parker. Baja California Norte: 1♂ 5♀, SIO, S arm of Bahía de los Angeles, 22-37 m, 26 April 1962, R. Rosenblatt. 5♂ 15♀, YPM, Bahía de los Angeles, 31-46 m, 13 May 1926, *Pawnee*. 1♂ 6♀, SIO, off San Felipe, 2 April 1973, C. Farwell. 4♂ 2♀, YPM, Bahía San Felipe, 19 May 1926, *Pawnee*. 6♂ 5♀, USNM, near northern end of Gulf of California, 9-18 m, February 1949, B. W. Walker. Sonora: 1♂ 1♀, USNM, Bahía de Adair, 46 m, 5 April 1968, Toral-García. 2♂ 3♀, USNM, Bahía de Adair, 29 m, 5 April 1978, Toral-García. 5♂ 13♀, USNM, off Bahía de San Jorge, 26 March 1967, shrimp trawler. 2♂ 1♀, INP, N of Guaymas, 26 April 1961, H. Chapa. 1♂, AHF, Bahía de Guaymas, 4-6 m, 22 January 1940. 1♀, SIO, Bahía de Guaymas, 22 March 1939, M. W. Johnson. 2♂, SIO, Bahía de Guásimas, 32 km S of Guaymas, April 1968, D. Hoese. Sinaloa: 1♂ 1♀, USNM, off Sinaloa, H. Chapa.

Sicyonia affinis Faxon 1893

Figures 35-38

Sicyonia affinis Faxon 1893:209 [syntypes: 1♂ 1♀, MCZ 4637, off Isla del Coco, Costa Rica, 5°31′30″N, 86°52′30″W, 100 fm (183 m), 28 February 1891, *Albatross* stn 3367; 1♂, USNM 21169, off Isla del Coco, Costa Rica, 5°32′45″N, 86°55′20″W, 52 fm (95 m), 28 February 1891, *Albatross* stn 3369; 2♀, USNM 21170, W of Isla de Malpelo, Colombia, 3°58′20″N, 81°36′00″W, 112 fm (205 m), 5 March 1891, *Albatross* stn 3378. 1♀, MCZ 4638, W of Isla de Malpelo, Colombia, 3°59′40″N, 81°35′00″W, 52 fm (95 m), 5 March 1891, *Albatross* stn 3379]. Faxon 1895:179, pl. 46, fig. 1, 1a-c. A. Milne Edwards and Bouvier 1909:244. De Man 1911:112. ?Chapa Saldaña 1964:9. Chirichigno Fonseca 1970:7, fig. 5. ?Rodríguez de la Cruz 1977: 12. Arana Espina and Méndez G. 1978:23, fig. 1-5. Méndez G. 1981:47, pl. 9, fig. 75-77. Pérez Farfante and Boothe 1981:424.

Eusicyonia affinis. Burkenroad 1934a:93, 1934b:126, 1938:84, fig. 24. Anderson and Lindner 1945:317.

Sicyonia penicillata Boone 1930:115 [part]. [Not *Sicyonia penicillata* Lockington 1879.]

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing one tooth posterior to level of hepatic spine and forming high crest behind posterior tooth. Rostrum short, not overreaching distal margin of eye. Abdomen lacking tubercles; second and third somites lacking inverted V-shaped ridges laterally; fifth somite with dorsomedian carina lacking tooth or sharp angle at posterior end. Petasma with distal projection of dorsolateral lobule compressed distally, its truncate tip produced dorsally in simple, minute spine. Thelycum with plate of sternite XIV without anteromedian tubercle and raised in paired low, but well-defined bulges. Branchiostegite lacking large mark.

Description.—Body relatively slender (Fig. 35) and lacking tubercles. Carapace studded with numerous short setae, those on anterior part of dorsum forming dense patches. First five abdominal somites with paired broad patches of short setae flanking dorsomedian carina; sixth with one in dorsolateral depression.

Rostrum short, reaching only as far as distal margin of eye, its length 0.25-0.35 cl; upturned to angle between 10° and 40°; armed with two dorsal teeth and three minute apical teeth; latter disposed on truncate apex with ventralmost one either terminal or subterminal; first dorsal tooth located distinctly anterior to orbital margin, second tooth situated at about anterior 0.25 cl of rostrum. Conspicuous adrostral carina, subparallel and distinctly dorsal to ventral margin, extending almost to end of rostrum.

Carapace with well-marked postrostral carina bearing two teeth; epigastric tooth, situated

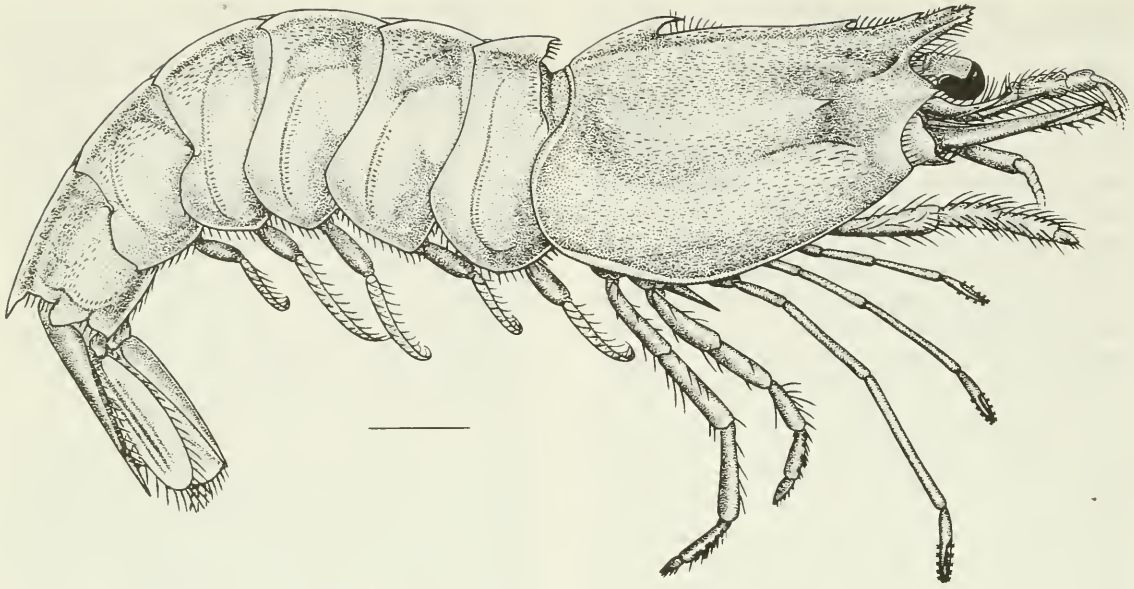


FIGURE 35.—*Sicyonia affinis* Faxon, ♀ 17 mm cl, 4.4 km off Isla Manuelita, Costa Rica. Lateral view. Scale = 5 mm.

slightly anterior to level of hepatic spine at about 0.15 cl from orbital margin, small, subequal to, or only slightly larger than first rostral tooth; and large posterior tooth, considerably larger than epigastric, hooklike, with apical portion acutely pointed and slightly curved anteriorly; tooth placed distinctly in advance of posterior margin of carapace, between 0.65 and 0.75 (mean 0.67) cl from orbital margin. Postrostral carina low anteriorly forming high crest descending gently from posterior tooth to posterior margin of carapace. Tuft of setae present at anterior base of each tooth. Antennal spine small, sharp, projecting from weakly developed buttress; hepatic spine moderately long and acutely pointed, situated at 0.20-0.25 (mean 0.22) cl from orbital margin; hepatic sulcus almost horizontal, accompanying inconspicuous carina; branchiocardiac carina broad, low, longitudinally disposed except for posterior part curving dorsally near posterior margin of carapace.

Antennular peduncle with stylocerite long, almost reaching level of mesial base of distolateral spine, its length about 0.95 distance between lateral base of first antennular article and mesial base of distolateral spine; latter reaching as far as distal 0.25 of second antennular article, antennular flagella short, mesial one more slender and longer, about 0.20 cl, than lateral, 0.16 cl.

Scaphocerite extending to distal end or slightly overreaching antennular peduncle; lateral rib produced distally in long, strong spine, surpassing margin of lamella. Antennal flagellum incomplete in specimens examined.

Third maxilliped stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with strongly marked dorsomedian carina extending from first through sixth somites, carina on first somite produced anteriorly in strong tooth (slightly more elevated than posterior tooth on carapace), its anterior margin subvertical but apical extremity slightly curved anteriorly; carina deeply cleft posteriorly on first five somites, on fourth and fifth not truncate but sloping gradually to apex of cleft, and on that of sixth somite produced in large, acute, posterior tooth.

First four somites with rounded or broadly angular anteroventral extremity unarmed; fourth somite with posteroventral extremity rounded and lacking spine, and that of fifth and sixth somites bearing minute spine.

First somite marked with short, weak, anteromedian pleural sulcus, its length slightly <0.2 distance from origin (emargination on anterior margin) to ventral margin of pleuron; united posterior tergal-posteromedian sulci relatively shallow. Second and third somites with weak anterior and posterior tergal sulci joining anterodorsally;

anteromedian pleural sulcus short, extending from slightly below midheight of somite to near ventral margin; posteromedian pleural sulcus with faint dorsal extension directed anteriorly at about 0.33 height of somite from dorsomedian line and just ventral to weak crescent-shaped ridge (latter delimited dorsally by tergal sulcus). Fourth somite with anterior tergal sulcus shallow and posterior tergal and posteromedian pleural sulci coalescent, extending from near base of dorsal carina to curve anteriorly near ventral margin. Fifth somite with united posterior tergal-posteromedian pleural sulci ending well above ventral margin. Sixth somite with strongly arched posterior pleural sulcus and low longitudinal ridge situated between base of middorsal carina and setose depression lying dorsal to weak cicatrix.

Telson with very weak median sulcus and bearing pair of small, fixed subterminal spines. Both rami of uropod extending as far as apex of telson or surpassing it by as much as 0.2 of their own lengths.

Petasma (Fig. 36*A*, *B*) with rigid distal projection of dorsolateral lobule curved mesially, raised proximodorsally in rounded prominence, and compressed distally; its truncate tip with ventral extremity rounded and dorsal extremity acutely produced in acute salient. Distal projection of ventrolateral lobule fleshy, with terminal part flattened (dorsal surface not bulbous) and curving dorsally.

Appendix masculina as illustrated in Figure 36*C*.

Thelycum (Fig. 37) with plate of sternite XIV, delimited by arched or straight lateral edges, rounded anteriorly, its surface raised in low, ovoid bulges separated by broad, median depression. Median plate of sternite XIII flask-shaped in outline, tapering gradually into long, slender spine reaching between midlength of coxae and proximal extremity of bases of second pereopods; plate incised and excavate at level of coxae of fourth pereopods; posterior component of plate with shallow posteromedian emargination. Sternite XI armed with paired short spines. Posterior thoracic ridge with concave anteromedian margin slightly overlapping plate of sternite XIV, ridge then flush with, or separated by shallow, transverse depression from sternite XIV.

Color.—"...light greenish yellow, banded with vermilion on the branchial regions and abdomen. Appendages red, antennary flagellum transversely banded with light and dark" (Faxon 1893).

Maximum size.—In the meager material avail-

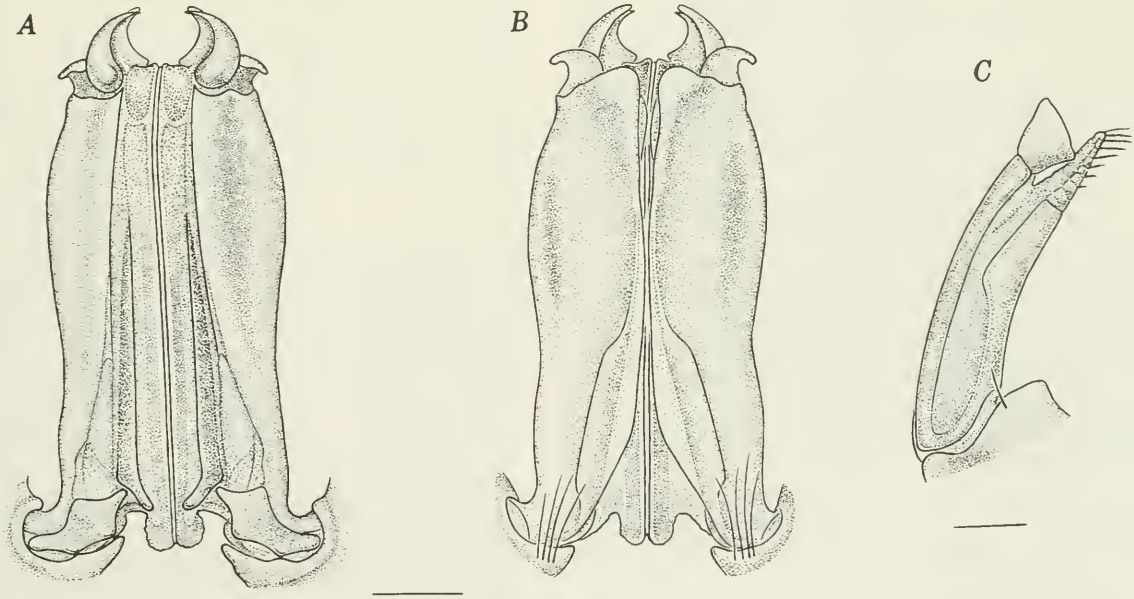


FIGURE 36.—*Sicyonia affinis*, ♂ 21.5 mm cl, 4.4 km off Isla Manuelita, Costa Rica. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scales = 1 mm.

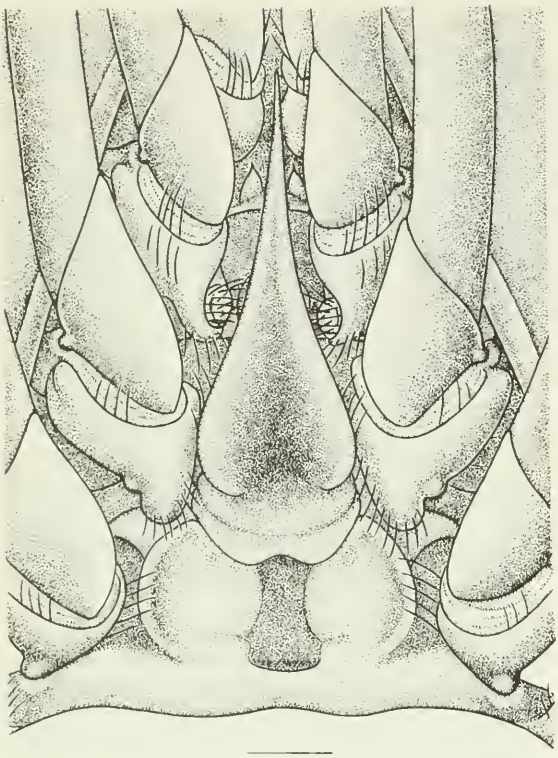


FIGURE 37.—*Sicyonia affinis*, ♀ 17 mm cl, 4.4 km off Isla Manuelita, Costa Rica. Thelycum. Scale = 1 mm.

able, larger male 21.5 mm cl, about 46 mm tl; largest female, 17 mm cl, about 62 mm tl.

Geographic and bathymetric ranges.—Known with certainty only from a restricted area between Isla Manuelita (5°34′N, 87°00′W), Costa Rica, and Isla de Malpelo (3°58′20″N, 81°36′00″W), Colombia (Fig. 38). Chirichigno Fonseca (1970) and Arana Espina and Méndez G. (1978) cited Paita, Peru, as the southern limit of the range of the species. Chirichigno Fonseca did not present a list of her material and Matilde Méndez G.[3] found no representative of the species in Peruvian collections, including those of the Instituto del Mar del Perú (IMARPE) from which Chirichigno Fonseca obtained most of her information. Chapa Saldaña (1964) recorded the occurrence of this species in the waters of Chiapas and Sinaloa, Mexico, but again, more recent studies, including the present one based on extensive material, failed to disclose its presence north of Costa Rica. Further investigations are necessary to ascertain the limits of the range of this shrimp both south of Isla de Malpelo and north of Isla Manuelita. *Sicyonia affinis* is one of only four members of the genus that have been recorded from the eastern Pacific off South America.

This species has been found at depths between 79-77 and 205 m, on substrates of rocks or broken shells.

Discussion.—*Sicyonia affinis* is one of the three closely related American Pacific species belonging to Burkenroad's (1934a) "*affinis* group" of his Division II. He characterized this group (in which he included *S. affinis* and *S. aliaffinis*, and to which

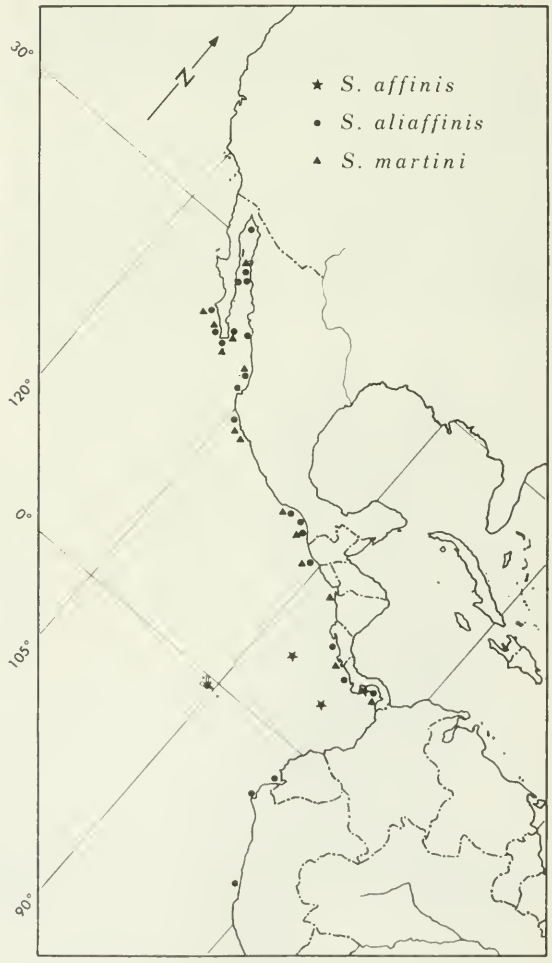


FIGURE 38.—Geographic distribution of *Sicyonia affinis*, *S. aliaffinis*, and *S. martini*.

[3]Matilde Méndez G., Instituto del Mar del Perú, Callao, Peru, pers. commun., January 1984.

recently Pérez Farfante and Boothe (1981) added *S. martini*) as possessing two teeth posterior to the orbital margin, of which one, that posterior to the level of the hepatic spine, is large. Like all members of Division II, in *S. affinis* the antennal spine is buttressed, but the buttress is barely distinct in contrast to that in *S. aliaffinis* and *S. martini* in which it is well developed. In *S. affinis* the first rostral tooth is situated farther anteriorly, at about the end of the anterior third of the rostral length from the orbital margin, than in the other two species in which it is placed opposite or immediately anterior to the orbital margin.

In *S. affinis* the abdominal surface is punctate but otherwise rather smooth, lacking tubercles, conspicuous ridges, and deep sulci. Also, in *S. affinis* the anteromedian sulcus of the first abdominal somite is not only weak but short, whereas in *S. aliaffinis* and *S. martini* it is deep (except ventrally in *S. martini* in which it is represented by a shallow depression) and long, in *S. aliaffinis* almost reaching the ventral margin of the pleuron. The anteromedian sulci of the second and third somites in *S. affinis* are distinct only ventrally, rather than dorsally as in *S. martini,* or along most of the height of the somite, as in *S. aliaffinis*. The posteromedian sulci of these somites in *S. affinis* extend dorsally only to a point situated at about 0.33 of the height of the somite from the dorsal midline where they turn anteriorly and are marked dorsally by weak longitudinal ridges; these sulci are considerably shorter than the well-incised ones in *S. aliaffinis*, which extend to about the dorsal 0.25 of the height of the somite, and are not accompanied dorsally by longitudinal ridges. In *S. martini* the posteromedian sulci curve anteroventrally at their dorsal ends, defining strong angular ridges.

As Burkenroad (1934a) pointed out, in *S. affinis* the dorsal carina of the fifth abdominal somite does not end in a sharp angle or acute tooth as it does in the other two species; instead its posterior part slopes gradually to the apex of the caudal cleft. In *S. affinis* the tip of the tooth on the first abdominal somite is slightly curved anteriorly whereas in *S. martini* it forms a conspicuous hook, and in *S. aliaffinis* the entire tooth is straight and projects anterodorsally. Furthermore, the anteroventral extremities of the pleura of the first four somites in *S. affinis* are unarmed whereas they bear a small spine in *S. aliaffinis*, and in *S. martini*, although lacking spines, are strongly angular instead of faintly so or rounded as they are in *S. affinis*.

These three species can also be distinguished readily by petasmal and thelycal characters. In *S. affinis* the projection of the dorsolateral lobule of the petasma, like that of *S. aliaffinis*, is truncate or shallowly emarginate distally and produced in a simple, dorsally directed, sharp salient, whereas in *S. martini* the projection curves gently to a conspicuously bifurcate, mesially directed tip; on the other hand, in *S. affinis*, as in *S. martini*, the projection of the ventrolateral lobule is flattened and curved or concave dorsally rather than being strongly bulbous as it is in *S. aliaffinis*. In the females of *S. affinis* and *S. martini* the thelycal plate of sternite XIV bears a pair of low but well-marked lateral bulges (longitudinally disposed in the former and transversely so in the latter), whereas in *S. aliaffinis* the plate is almost flat or barely raised in ill-defined elevations. Moreover, in both *S. affinis* and *S. aliaffinis*, the posterior emargination of the median plate of sternite XIII does not embrace a tubercle, as it does in *S. martini*.

Material.—17 specimens from 6 lots.

Costa Rica—3♂ 5♀, AHF, 4.4 km off Isla Manuelita, 146 m, 3 June 1973, *Velero IV* stn 19044. 1♂, syntype, USNM, off Isla del Coco, 95 m, 28 February 1891, *Albatross* stn 3369. 1♂ 1♀, syntypes, MCZ, off Isla del Coco, 183 m, 28 February 1891, *Albatross* stn 3367.

Panama—3♀, USNM, NE of Isla Iguana, 79-77 m, 4 May 1967, *Pillsbury* stn 515.

Colombia—1♀, syntype, MCZ, W of Isla de Malpelo, 95 m, 5 March 1891, *Albatross* stn 3379. 2♀, syntypes, USNM, W of Isla de Malpelo, 205 m, 5 March 1891, *Albatross* stn 3378.

Sicyonia aliaffinis (Burkenroad 1934)

Figures 38-42

Eusicyonia aliaffinis Burkenroad, 1934a:92, fig. 24 [holotype ♂, YPM 4393; type-locality: Pacific coast of southern Mexico (NW of Puerto Madero), 14°48′40″N, 92°54′40″W, 19-30 fm (35-55 m), 9 April 1926, *Pawnee*]. Burkenroad 1938:84, fig. 25, 27. Anderson and Lindner, 1945:317.

Eusicyonia sp. Castro, 1966:17 [in part, by implication].

Sicyonia aliaffinis. Chapa Saldaña 1964: 15. Bayer et al. 1970:A97. Chirichigno Fonseca 1970:7, fig. 6. Del Solar 1972: 7. Rodríguez de la Cruz 1977:10. Arana Espina and Méndez G. 1978:25, fig. 6-9.

Anonymous 1980:7. Brusca 1980:256. Sosa Hernández et al. 1980:12. Méndez G. 1981:47, pl. 9, fig. 78-82. Pérez Farfante and Boothe 1981:424. Pérez Farfante 1982:370.

Vernacular names: rock shrimp, target shrimp, Japanese shrimp (United States); camarón de piedra, camarón de roca, camarón japonés, cacahuete (Mexico); camarón conchiduro (Mexico, Panama); camarón de mar, camarón cascaradura (Peru). FAO names: hardhusk rock shrimp (English); camarón cáscara dura (Spanish); boucot noisette (French).

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing one tooth posterior to level of hepatic spine and raised in high crest behind posterior tooth. Rostrum short, not overreaching distal margin of eye. Abdomen tuberculate; second and third somites not bearing special inverted V-shaped ridges laterally; fifth somite with dorsomedian carina ending in sharp angle or tooth posteriorly. Petasma with distal projection of dorsolateral lobule compressed distally, its truncate tip produced dorsally in simple, minute spine. Thelycum with plate of sternite XIV lacking anteromedian tubercle and either flat or barely raised in ill-defined bulges. Branchiostegite bearing large, horizontally disposed 9-shaped color pattern.

Description.—Body relatively short (Fig. 39). Carapace with irregular patches of longer setae on dorsum, in depression delimiting branchiocardiac carina posterodorsally, and on areas anterior to hepatic spine and ventral to hepatic sulcus; one patch also present in dorsolateral depression of sixth abdominal somite. Abdomen rather heavily granulate on first three abdominal somites, usually slightly so on last somites.

Rostrum short, not overreaching distal margin of eye, its length increasing linearly with carapace length (Fig. 40) to about 16 mm cl, then increasing little, not surpassing 6 mm (proportional length decreasing with increasing size from as much as 0.43 to as little as 0.20 cl); subhorizontal or upturned to 30° in males and to 50° in females; armed with two dorsal teeth and three (occasionally two) apical ones, latter disposed on obliquely truncate apex, upper tooth posterior to level of ventral one (occasionally appearing to be third of dorsal series); first dorsal tooth subequal to or, more often slightly smaller than, epigastric and situated opposite or immediately anterior to orbital margin; second tooth variably placed between anterior 0.17 and 0.40 (mean 0.30) rl. Conspicuous adrostral carina, subparallel and near ventral margin, ex-

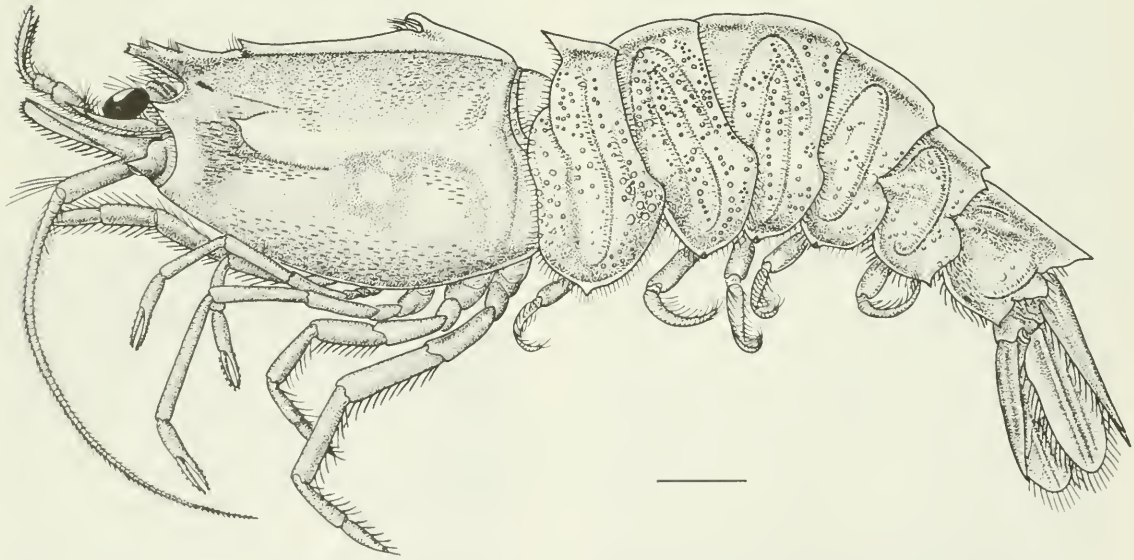


FIGURE 39.—*Sicyonia aliaffinis* (Burkenroad 1934), ♀ 26 mm cl, west of Puerto Madero, Golfo de Tehuantepec, Mexico. Lateral view. Scale = 5 mm.

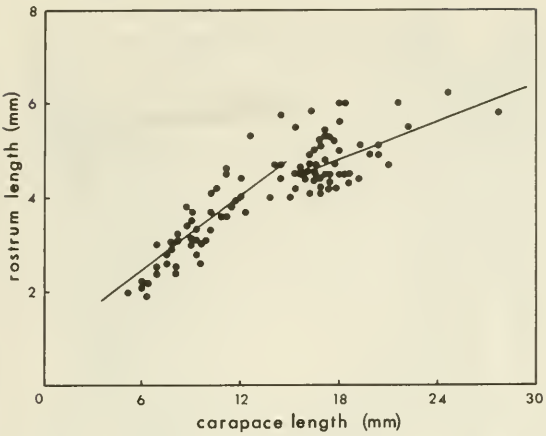


FIGURE 40.—*Sicyonia aliaffinis*. Relationship between rostrum length and carapace length (regression equation for specimens with about 16 mm cl or less, $y = 0.83950 + 0.25635x$; regression equation for those larger, $y = 2.34086 + 0.13665x$).

tending from orbital margin almost to end of rostrum.

Carapace with strong postrostral carina bearing two teeth: 1) epigastric tooth small, subequal to or slightly larger than first rostral tooth, situated opposite or anterior to level of hepatic spine, between 0.15 and 0.22 (mean 0.18) cl from orbital margin; and 2) posterior tooth, much larger, as much as three times higher than epigastric, hooklike, its apical portion acutely pointed and strongly curved anteroventrad; tooth placed well in advance of posterior margin of carapace, between 0.66 and 0.76 (mean 0.71) cl from orbital margin. Postrostral carina slightly elevated just in front of posterior tooth and forming high crest from latter descending gently to posterior margin of carapace. Tuft of setae present at anterior base of each tooth. Antennal spine sharp, projecting from well-marked buttress; hepatic spine acute, larger than antennal, arising from raised area, and situated between 0.19 and 0.26 (mean 0.23) cl from orbital margin. Postocular sulcus deep anteriorly, continuing posteriorly as low groove; hepatic sulcus well marked; branchiocardiac carina distinct but rather low, extending longitudinally from hepatic region almost to posterior margin of carapace, there bifurcating: one branch curving dorsally and other disposed ventrally.

Antennular peduncle with stylocerite produced in long spine, its length about 0.9 distance between lateral base of first antennular article and mesial base of distolateral spine; latter extending to about midlength of second article.

Scaphocerite almost reaching or slightly overreaching distal margin of antennular peduncle; lateral rib produced distally in long, strong spine surpassing distal margin of lamella. Antennal flagellum as much as 2 times as long as carapace.

Abdomen with high dorsomedian carina extending from first through sixth somites, carina on first somite produced in strong triangular tooth as high as, or usually higher (as much as one-third) than, posterior tooth on carapace, its anterior margin straight, subvertical or sloping anterodorsally; carina on fourth somite obliquely truncate posteriorly forming obtuse (rarely almost right angle); that on fifth strongly truncate forming acute posterior tooth; and that on sixth strongly produced in large acute posterior tooth.

First four somites with angular anteroventral extremity bearing small spine; fourth somite with posteroventral extremity broadly angular, occasionally armed with minute spine, and fifth and sixth somites with posteroventral extremity bearing small sharp spine, that of fifth slightly larger.

First somite marked with long anteromedian pleural sulcus joining coalescent posterior tergal-posteromedian pleural sulci near margin of pleuron. Second and third somites with deep anterior and posterior tergal and long, well-incised anteromedian (expanding ventrally) and posteromedian pleural sulci, posteromedian ones extending dorsally to a point located at least at 0.25 of the height of the somite from the dorsal midline. Fourth somite bearing anterior and posterior tergal sulci, posterior one merging with deep, long posteromedian sulcus. Fifth somite marked with anterior tergal sulcus and united posterior tergal-posteromedian pleural sulci. Sixth somite with short anterior tergal sulcus, strongly arched posterior pleural one, and setose, longitudinal depression delimited dorsally by rib and ventrally by usually strong cicatrix.

Telson with pair of small but well-developed fixed spines. Rami of uropod subequal in length, reaching or slightly overreaching apex of telson.

Petasma (Fig. 41) with rigid distal projection of dorsolateral lobule curved mesially, raised proximodorsally in rounded prominence, and compressed distally; its truncate tip with ventral extremity rounded and dorsal extremity sharply produced in minute spine. Fleshy distal projection of ventrolateral lobule with firm, terminal part directed laterally almost at right angle, dorsally bulbous, ventrally flat, and tapering to pointed, ventrally inclined apex.

Petasmal endopods coupled in males 8.2 mm cl,

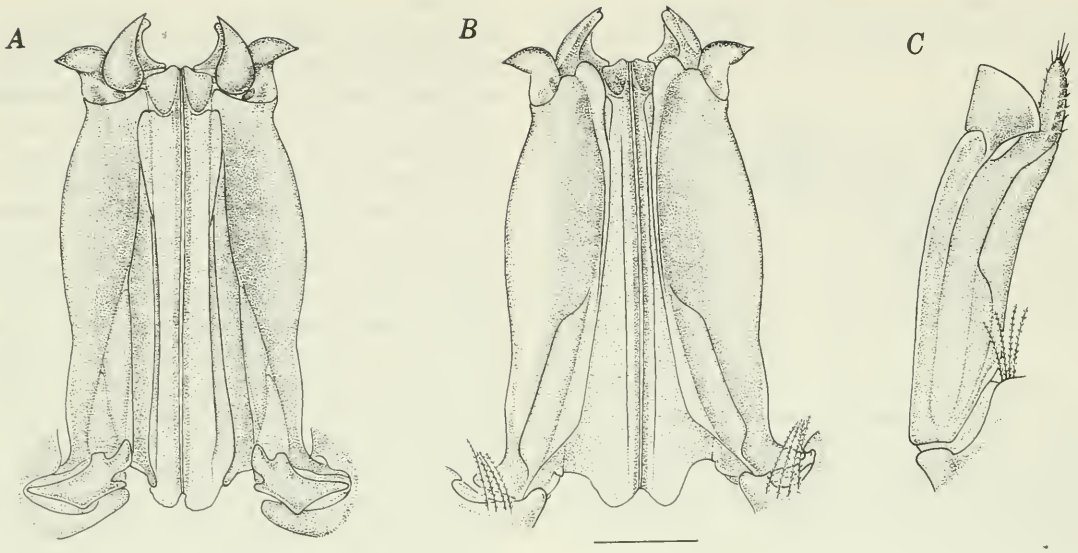


FIGURE 41.—*Sicyonia aliaffinis*, ♂ 16 mm cl, west of Puerto Madero, Golfo de Tehuantepec, Mexico. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scale = 1 mm.

about 27 mm tl, but may not be joined in individuals as much as 11 mm cl, about 36 mm tl.

Appendix masculina as illustrated in Figure 41*C*.

Thelycum (Fig. 42) with plate of sternite XIV, delimited anterolaterally by strongly convex margins, flat or very slightly raised in paired ill-defined bulges flanking depressed median portion. Median plate of sternite XIII flask-shaped in outline, tapering gradually into long, slender spine reaching as far as distal margin of coxae of anteriorly extended second pereopods; posterior component of plate with posterolateral margins strongly arched and separated by median emargination variable in width. Sternite XI armed posteriorly with paired short spine. Posterior thoracic ridge with weakly concave or virtually straight anteromedian portion slightly elevated, but areas lateral to it merging indistinctly with plate of sternite XIV.

The smallest impregnated female encountered has a carapace of 5 mm, about 23 mm tl.

Color.—Specimens from Peruvian waters were described by Arana Espina and Méndez G. (1978) as follows: dorsum dark, petroleum green; carapace lighter laterally, exhibiting various shades of gray, green, or pink, and bearing striking dark mark resembling longitudinally disposed "9" on branchial region. Antennae with light and dark

FIGURE 42.—*Sicyonia aliaffinis*, ♀ 25 mm cl, west of Puerto Madero, Golfo de Tehuantepec, Mexico. Thelycum. Scale = 2 mm.

bands. Pereopods and pleopods pink. In addition, spot—dark proximally, intense blue distally—present on lateral ramus of uropods. Sosa Hernández et al. (1980) also presented color notes on specimens from the Golfo de Tehuantepec: body cream, suffused with reddish brown; carapace bearing hook-shaped brown mark on each side; lateral ramus of uropod with violet ventral spot; antennae banded with violet with cream. In Anonymous' (1980) work on the crustacean decapods of the Gulf of California, the "9" is described as purplish brown.

Maximum size.—Male, 22.0 mm cl, 86.6 mm tl; female, 28.5 mm cl, 100.7 mm tl (both recorded by Arana Espina and Méndez G. 1978). Largest individuals examined by me: male, 21.4 mm cl, about 71 mm tl; female, 28 mm cl, about 89 mm tl.

Geographic and bathymetric ranges.—Isla Santa Margarita (24°20′00″N, 111°45′30″W - 24°20′10″N, 111°46′40″W), Baja California Sur, Mexico, to Cabo San Lucas, in the southern part of the Gulf of California along both the east and west coasts, and southward to Bahía Chamela (19°34′00″N, 105°07′24″W), Jalisco. Also from off Salina Cruz (16°10′00″N, 95°00′00″W), Oaxaca, Mexico, to Santa María (12°24′S), Peru, except off middle Central America, Colombia, and most of Ecuador. In the waters of Ecuador, it has been recorded from the Golfo de Guayaquil and Islas Galápagos (Fig. 38). This species has been found at depths between 4-9 and 242 m, mostly at <85 m, on substrates of sand and mud.

The report of the occurrence of this shrimp in Santa María, Peru, (Vélez J., J. Zeballos, and M. Méndez G., in press) is the first from waters south of Bahía Sechura (5°43.1′S, 81°05.0′W), the southernmost record cited by Arana Espina and Méndez G. (1978). These specimens from Santa María were collected at a depth of 10.5 m by A. Robles on 28 June 1983.

Discussion.—The closest relative of *S. aliaffinis* is *S. affinis*. The former, however, reaches a larger size (about 29 mm cl) than *S. affinis*, the largest known specimen of which has only a 17 mm cl. *Sicyonia aliaffinis* also differs from *S. affinis* in having a strongly buttressed antennal spine and in the position of the first dorsal rostral tooth, which is situated opposite or barely anterior to the orbital margin instead of at about the anterior end of the basal third of the rostrum.

Differences in the abdominal characters are even more striking. In *S. aliaffinis* the abdomen is granulose, heavily so on the first three somites, and the transverse sulci are deeply incised whereas in *S. affinis* it is glabrous and bears weak sulci, some of which are incomplete, adding to the smooth appearance of the abdomen. In *S. aliaffinis* the anteromedian sulcus of the first somite is long, and although it becomes shallow ventrally, it extends to near the ventral margin of the pleuron; in *S. affinis*, in contrast, it is short, ending considerably above the ventral margin of the pleuron. The anteromedian sulci of the second and third somites in *S. aliaffinis* are long instead of short, recognizable only on the ventral half of the somites; the posteromedian sulci of these somites in *S. aliaffinis* extend dorsally to a point at least at 0.25 of the height of the somite from the dorsal midline and do not turn anteriorly, whereas in *S. affinis* they extend only to about 0.35 from the dorsal midline and turn anteriorly, delimiting ventrally a weak longitudinal ridge which is absent in *S. aliaffinis*. Also in *S. aliaffinis*, the anterior tooth of the first somite is acute but not curved at the tip as it is in the other species, and the dorsal carina of the fifth somite ends in a sharp angle or more often in a tooth, whereas in *S. affinis* it slopes gradually to the base of the caudal cleft. The anteroventral extremities of the first through fourth pleura in *S. aliaffinis* bear a small spine rather than being unarmed.

Features of the external genitalia also allow a ready separation of these two species. In *S. aliaffinis*, the distal projection of the ventrolateral lobule of the petasma is bulbous dorsally; in contrast, that of *S. affinis* is comparatively thin. The thelycal plate of sternite XIV is flat or very faintly raised laterally in ill-defined elevations in *S. aliaffinis*, whereas in *S. affinis* it bears a pair of low but well-marked ovoid or subelliptical bulges.

In addition to the morphological characters discussed above, *S. aliaffinis* exhibits a striking 9-shaped color pattern on the branchial region which distinguishes it from all of its congeners occurring in the American Pacific.

Discussing the diagnostic characters of *S. aliaffinis*, Burkenroad (1934a) stated that "The carina of the second somite is, although not notched above the juncture of the tergal sulci, shallowly emarginate at this point." I have observed that this carina may be entire or slightly depressed either at the point where Burkenroad noted it or more posteriorly; consequently, in this shrimp the contour of the carina is insignificant.

Remarks.—Arana Espina and Méndez G. (1978) graphed the size distribution of each sex in samples of this shrimp from the Golfo de Guayaquil. They included correlations between carapace length and total length, total weight, and abdominal weight. They determined that the relative growth rate in males is higher than that in females, and that within the size range of the shrimp studied, eight molts occurred with an increase of 7.25% at each molt.

Although Castro (1966) did not cite *S. aliaffinis* by name, he stated that among the specimens of "*Eusicyonia*" collected off Puerto Peñasco and near Isla de San Jorge, Sonora, Mexico, there were some bearing a 9-like shaped spot, which undoubtedly indicates that they belonged to this species.

Commercial importance.—*Sicyonia aliaffinis*, like the other six relatively large species of the genus occurring in the American Pacific, is frequently taken together with other penaeoids of greater economic value. In the Gulf of California it is present in the commercial catches made on the eastern side. In some other areas along its range, e.g., the Golfo de Guayaquil (Arana Espina and Méndez G. 1978), it is found in quantities that might support development of a fishery.

Material.—251 specimens from 27 lots.

Mexico—Baja California Sur: 2♂ 1♀, SIO, SW of Isla Santa Margarita, 29-40 m, 13 November 1964, *Black Douglas*. 1♂, SIO, NW of Todos Santos, 38 m, 9 November 1964, *Black Douglas*. 1♂, YPM, Bahía San Lucas, 24 m, 7 May 1936, *Zaca* stn 135D-26. 1♂ 1♀, USNM, W of Estero de los Algodones, 47 m, 3 April 1978, Toral García. 1♂, YPM, Bahía Santa Inés, 37 m, 10 April 1936, *Zaca* stn 141-D4. Nayarit: 57♂ 38♀, SIO, NE of Isla María Madre, 51 m, 31 March 1973, *Agassiz*. 15♂ 8♀, SIO, NE of Isla María Madre, 55 m, 31 March 1973, *Agassiz*. Jalisco: 1♀, USNM, Puerto Vallarta, 13 April 1937. 2♀, SIO, N part of Bahía Chamela, 15-18 m, 2 April 1973, *Agassiz*. Oaxaca: 13♂ 13♀, USNM, E of Salina Cruz, Golfo de Tehuantepec, 18 m, 10 July 1963, I. Mayés A. 2♂ 1♀, SIO, Golfo de Tehuantepec, 55 m, 6 June 1965, T. Matsui. 1♀, USNM, Laguna Lagartero, Ixhuatán, 25 July 1963, G. Solórzano. Chiapas: 2♂ 1♀, USNM, Puerto Arista, 14 January 1964, I. Mayés A. 8♂ 8♀, SIO, Golfo de Tehuantepec, 46-48 m, 10 April 1973, *Agassiz*. 3♂ 2♀, SIO, Golfo de Tehuantepec, 73 m, 10-11 July 1963, D. Dockins. 1♂, holotype, YPM, off "southern Mexico" [NW of Puerto Madero], 35-55 m, 9 April 1926, *Pawnee*. 17♂ 38♀, SIO, W of Puerto Madero, Golfo de Tehuantepec, 55 m, 10 April 1973, *Agassiz*.

Guatemala—1♂, AHF, off San José light, 42 m, 23 March 1939.

Costa Rica—1♂, USNM, near Quepos, 242 m, 26 April 1973, *Enriqueta*.

Panama—1♂, AHF, Isla Taboga, 4-9 m, 2 May 1939. 1♂, USNM, Bahía Santelino, 1.6 km N of Punta de Cocos, Archipiélago de las Perlas, 9 February 1939. 1♀, USNM, S of Isla del Rey, 44-42 m, 7 May 1967, *Pillsbury* stn 551. 1♀, USNM, SW of Bahía San Miguel, 55 m, 7 May 1967, *Pillsbury* stn 549. 2♂ 1♀, USNM, 12 km NW of Punta Caracoles, Darién, 84 m, L. G. Abele.

Ecuador—1♀, USNM, S of Isla Seymour, Galápagos, 7-13 m, 9 March 1938, F. E. Lewis. 1♀, USNM, off Playas, Golfo de Guayaquil, 16 m, 1976, P. Arana Espina.

Peru—1♂, USNM, off Caleta Cruz, 10-14 m, 1970, E. Valdivia.

Sicyonia martini Pérez Farfante and Boothe 1981

Figures 38, 43-46

Eusicyonia species, Burkenroad 1938:81, fig. 26, 28-30.

Sicyonia martini Pérez Farfante and Boothe 1981:424, fig. 1-4 [holotype ♀, USNM 180235; type-locality: SW of Punta Ana María, Golfo de Panama, 7°50′30″N, 78°49′00″W, 58 m, *Pillsbury* stn 556].

Vernacular names: rock shrimp (United States); camarón de piedra, camarón de roca (Mexico); camarón conchiduro (Mexico, Panama).

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing one tooth posterior to level of hepatic spine and raised in high crest behind posterior tooth. Rostrum long, conspicuously overreaching distal margin of eye. Abdomen tuberculate; second and third somites bearing unusual inverted V-shaped ridges laterally; fifth somite with dorsomedian carina sharply truncate posteriorly. Petasma with distal projection of dorsolateral lobule tapering distally to minutely bifurcate tip, arms sharp. Thelycum with plate of sternite XIV bearing anteromedian tubercle. Branchiostegite without 9-shaped color pattern.

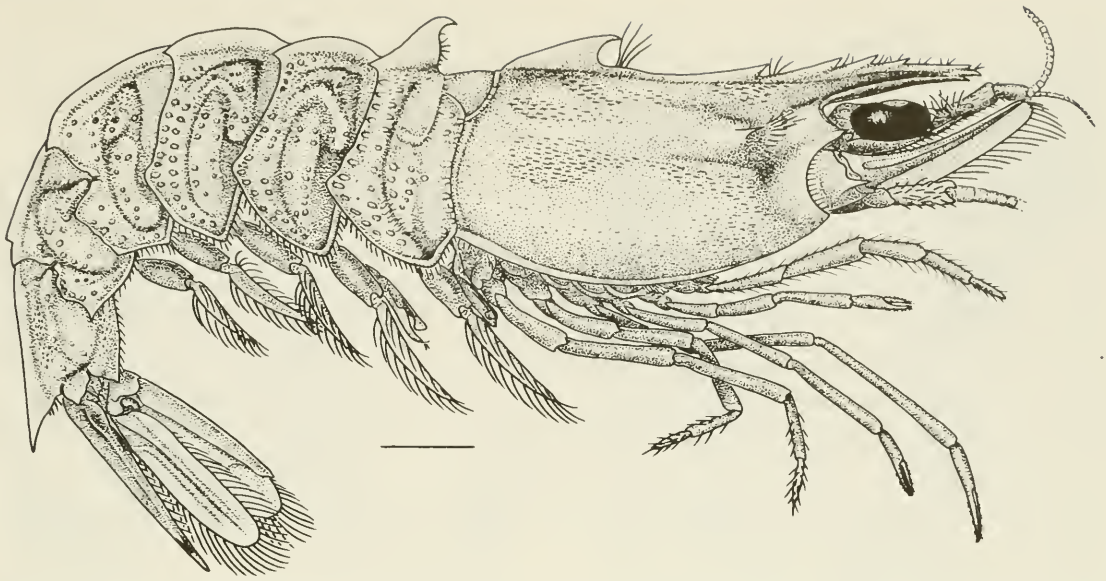


FIGURE 43.—*Sicyonia martini* Pérez Farfante and Boothe (1981), paratype ♂ 19 mm cl, off Puerto Escondido, Golfo de Panamá. Lateral view. Scale = 5 mm.

Description.—Body relatively slender (Fig. 43). Carapace with sparse long setae intermingled with elongate patches of shorter ones situated on dorsum, ventral to hepatic sulcus, posterior to pterygostomian region, and on posterodorsal part of branchiostegite; patches also present on abdominal terga. Abdomen tuberculate, tubercles numerous on first five somites, few on sixth.

Rostrum comparatively long, conspicuously surpassing eye, reaching as far as distal 0.33 of second antennular article, its length, 0.40-0.54 cl, increasing linearly with carapace length (Fig. 44); armed with two or three dorsal teeth and cluster of apical teeth, both groups varying in disposition and number in males and females. In males, rostrum horizontal or directed upward at slight angle of no more than 10°, but weakly decurved at tip, with three dorsal teeth evenly spaced; first rostral tooth situated immediately anterior to orbital margin, last usually separated from upper apical tooth by interval (about 0.33 rl) slightly greater than that between dorsal teeth; apical cluster consisting of three or four teeth (76% and 24%, respectively), with subterminal ventral tooth situated not far from adjacent apical tooth. In females, rostrum strongly elevated at angle of 40°-50°, its ventral margin straight or, more often, strongly convex along midlength, and with two dorsal teeth; first rostral tooth placed distinctly anterior to orbital margin; interval between second tooth and upper apical tooth slightly shorter than that between first and second; apical cluster consisting of three, four, or five teeth (1, 87, and 12%, respectively), ventral one subterminal, distinctly removed from adjacent apical tooth; teeth of apical

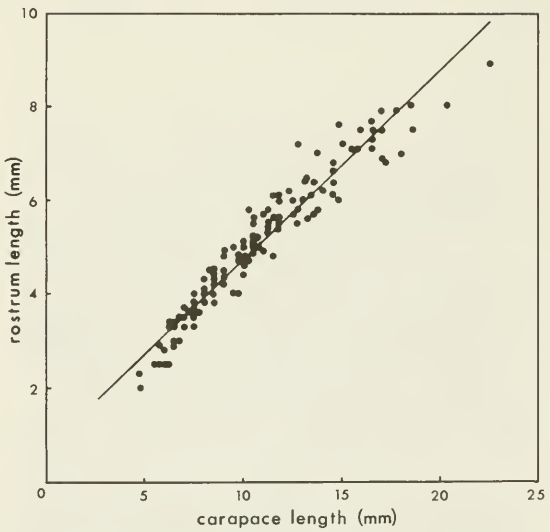


FIGURE 44.—*Sicyonia martini*. Relationship between rostrum length and carapace length (regression equation, $y = 0.76705 + 0.39436x$).

cluster either turned ventrally, or less frequently directed forward. Adrostral carina strong, sometimes sharp, reaching between level of last apical tooth and base of ventral apical one.

Carapace with postrostral carina well-marked, bearing two teeth: 1) epigastric tooth, small, subequal to first rostral tooth, situated opposite or only slightly anterior to hepatic spine; and 2) posterior tooth, placed between 0.63 and 0.73 (mean 0.69) cl from orbital margin, large, about three times as high as epigastric tooth, hooklike at tip; postrostral carina low anteriorly, slightly elevated below apex of posterior tooth, and forming crest from latter descending gently toward ridge on posterior margin of carapace; each tooth preceded by tuft of long setae. Antennal spine small, projecting from rather long buttress; hepatic spine acutely pointed, much longer than antennal, arising from moderately raised area, and situated between 0.14 and 0.20 (mean 0.18) cl from orbital margin. Postocular sulcus short but deep anteriorly, continuing posteriorly as weak groove; hepatic sulcus deep, subhorizontal, accompanying inconspicuous carina. Branchiocardiac carina low but clearly distinct, long, extending from base of hepatic region to near posterior margin of carapace, then curving dorsally toward base of posterior tooth.

Antennular peduncle with stylocerite produced in spine distally, extending about 0.8 distance between lateral base of first antennular article and mesial base of distolateral spine; distolateral spine strong, reaching as far as midlength of second article; antennular flagella short, mesial one slightly shorter than lateral.

Scaphocerite almost reaching (occasionally overreaching) distal end of antennular peduncle; length of antennal flagellum as much as 2.5 times cl.

Third maxilliped slightly stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with high dorsomedian carina extending from first through sixth somites; carina on first somite produced in large, apically hooked, triangular anterior tooth, more elevated than posterior tooth on carapace; carina of fifth somite abruptly truncate posteriorly; and that of sixth produced in large, acute posterior tooth.

Anteroventral margin of pleuron of first abdominal somite barely to distinctly concave; anteroventral angle 90°-100°, that of third and fourth 90° or less, with vertex slightly produced anteroventrally; pleuron of fifth roughly pentagonal, anteroventral and posteroventral angles with vertices slightly produced, posteroventral one often armed with small spine; posteroventral angle of pleuron of fifth and sixth somites armed with spine, that of fifth larger.

First somite with anteromedian sulcus well defined only dorsally but continuing ventrally as shallow depression joining deep posterior tergal-posteromedian pleural sulcus, ridge often extending posteriorly from ventral portion of anteromedian pleural sulcus to fused posterior sulci. Second and third somites with relatively short, anterior and posterior tergal sulci; short anteromedian pleural sulcus merging ventrally with conspicuous broad depression, latter terminating near anteroventral margin of corresponding pleuron; posteromedian pleural sulcus extending dorsally to about 0.3 height of somite measuring from middorsal line, there curving anteriorly; special inverted V-shaped ridge lying between tergal and pleural sulci. Fourth somite with anterior tergal and long, united posterior tergal-posteromedian pleural sulci; anteroventral part of latter curving dorsally; often short longitudinal ridge present at about 0.3 height of somite from middorsal line. Fifth somite with anterior tergal sulcus continuous with united posterior tergal-posteromedian pleural sulci, anteroventral portion of latter fading as shallow depression; cicatrix extending posteriorly from ventral end of anterior tergal sulcus. Sixth somite with arched posterior pleural sulcus and with shallow setose depression situated dorsal to long but interrupted strong cicatrix.

Telson with pair of small, fixed, subterminal spines. Both rami of uropod reaching, or almost reaching apex of telson.

Petasma (Fig. 45*A, B*) with rigid distal projection of dorsolateral lobule strongly curved mesially, raised proximodorsally in subhemispheric prominence, and ending in bifurcate apex, both tips sharp. Fleshy distal projection of ventrolateral lobule falling short of adjacent one, and with terminal part truncate and curved dorsally.

Petasmal endopods coupled in males as small as 5.8 mm cl, about 23 mm tl, but may not be joined in individuals as large as 9 mm cl, about 32 mm tl.

Appendix masculina as illustrated in Figure 45*C*.

Thelycum (Fig. 46*A, B*) with plate of sternite XIV forming slightly to broadly rounded lateral flanges partly surrounding and merging with roughly semicircular, low mesial bulges; latter separated by median depression bearing oval or, occasionally, subhemispheric anterior tubercle (if

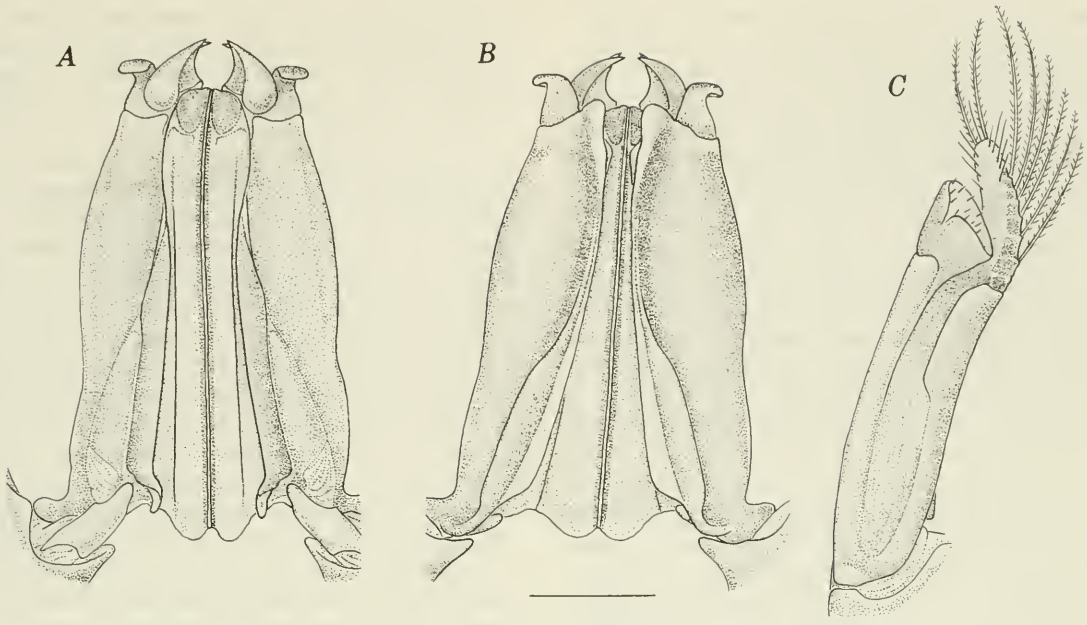


FIGURE 45.—*Sicyonia martini*, paratype ♂ 13.7 mm cl, south of Archipiélago de las Perlas, Golfo de Panamá. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scale = 1 mm.

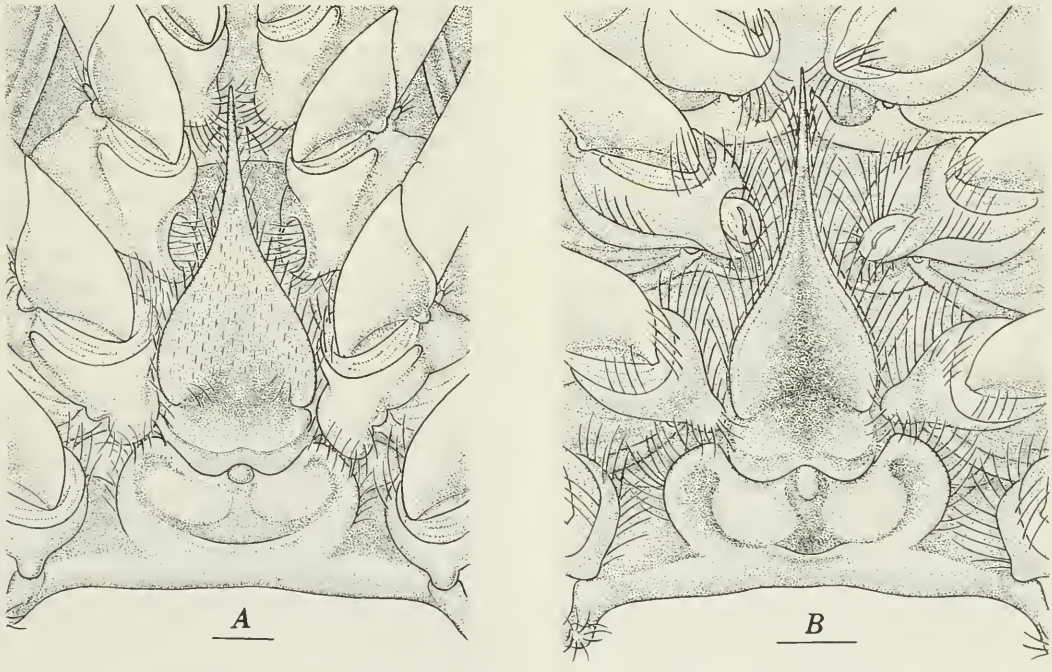


FIGURE 46.—*Sicyonia martini*. *A*, holotype ♀ 21 mm cl, southwest of Punta Ana María, Golfo de Panamá; *B*, ♀ 16.5 mm cl, Banco Gorda de Afuera, Baja California Sur. Thelyca. Scales = 1 mm.

oval, long axis disposed either longitudinally or transversely). Median plate of sternite XIII flaskshaped in outline, tapering into long, slender spine reaching between anterior and posterior extremities of coxa of anteriorly extended second pereopods; plate constricted, its ventral surface strongly excavate at level of coxae of fourth pereopods; posterior component of plate, with rounded posterolateral margins and broad shallow, median emargination. Paired, broad based spines projecting anteriorly from posterior margin of sternite XI. Posterior thoracic ridge narrow, with concave, sharp anteromedian margin but merging laterally with preceeding plate.

The smallest impregnated females encountered have a carapace of 8 mm, about 31 mm tl.

Color.—Specimens preserved in Formalin[4] buff with purplish blue markings: antenna, lateral ridge of scaphocerite, postrostral and abdominal carina, and dorsal ribs of telson transversely banded; anterior margin and posterior ridge of carapace, anterior margin of pleuron of first abdominal somite, and posterior margin of all abdominal somites with series of small spots; tip of teeth on rostrum, carapace, and first abdominal somite also purplish blue; lateral ramus of uropod with subterminal spot on lateral ridge and large mesial blotch at same level.

Maximum size.—Males 15.6 mm cl, 60.5 mm tl; females 22.5 mm cl, 87.2 mm tl.

Geographic and bathymetric ranges.—From southwest of Isla Santa Margarita (24°19′48″ N, 111°47′06″W - 24°19′36″N, 111°47′06″W), Baja California Sur, Mexico, to southern tip of Baja California Sur and throughout the Gulf of California southward to off Punta Lizardo (18°06′00″N, 102°57′18″W), Michoacán; also from E of Puerto Angel (15°41′00″N, 96°07′30″W), Oaxaca, Mexico, to SW of Punta Ana María (7°50′30″N, 78°49′00″W - 7°50′48″N, 78°48′00″W), Panama (Fig. 38). It has been found at depths between 9 and 242 m, on substrates of sand, rock, mud, and coralline debris.

Discussion.—Although closely allied to *S. affinis* and *S. aliaffinis*, *S. martini* can be distinguished readily from both of them by the length, shape, and armature of the rostrum; the shape of the tooth on the first abdominal somite; the sculpture of the abdomen; and features of the petasma and thelycum.

In *S. martini* the rostrum is quite long, surpasses the eyes, and almost reaches the distal margin of the second antennular article. In males, the rostrum is straight or upturned at an angle of no more than 10°, and armed with three dorsal teeth and three or four apical teeth, the ventral one of which is occasionally subterminal. In females, the rostrum is strongly elevated (40°-50°), with its ventral margin usually markedly convex in the middle and concave posterior to the base of the subterminal tooth, and bears two dorsal teeth and three to five apical teeth, the ventral one of which lies distinctly posterior to the adjacent tooth. In *S. affinis* and *S. aliaffinis* the rostrum is shorter than in *S. martini*, reaching at most the distal margin of the eye; in both males and females it is upturned at an angle of about 30°, thus more elevated than in males of *S. martini* but less so than in females, and its ventral margin is usually straight or, occasionally, slightly convex basally. Also, in these two species the rostrum is armed with only two dorsal teeth, and the ventral of the two or three apical teeth (four or five have not been observed) is terminal, instead of subterminal as it is in all females and some males of *S. martini*.

The tooth on the first abdominal somite is proportionately higher in *S. martini* than in the other two species; its dorsal margin is sigmoid and it ends in a strong, recurved, hooklike tip. In *S. affinis* and *S. aliaffinis* the dorsal margin of the tooth is gently curved in an arc, and the tooth is inclined more anteriorly than in *S. martini*; in *S. affinis* it ends in a slightly curved tip, and in *S. aliaffinis* the tip is triangular rather than hooklike. Also, the abdominal sculpture of *S. martini* is much stronger than that of its two closest congeners, and exhibits unusual, longitudinally disposed, inverted V-shaped ridges at the ventral end of the dorsal third of the second and third somites, which are absent in the other two species.

In *S. martini*, the projection of the dorsolateral lobule of the petasma is bifurcate apically, the tips sharp. In *S. affinis* and *S. aliaffinis*, the projection is compressed distally with the ventral extremity rounded, the dorsal extremity sharply produced in a simple spine, and the distal margin (immediately ventral to the spine) truncate or slightly emarginate. Furthermore, the projection of the ventrolateral lobule of the petasma of *S. martini*, like that of *S. affinis* but in contrast to that of *S. aliaffinis*, is flattened distally rather than thickened (dorsally) into a subovoid pro-

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tuberance. The females of *S. martini* differ from those of all the other *Sicyonia* occurring in the region by possessing a conspicuous tubercle on the anteromedian extremity of the plate of sternite XIV.

In addition to the distinguishing characters cited above, *S. martini* exhibits other features that differ from those of *S. affinis*. The dorsomedian carina of the fifth abdominal somite is abruptly truncate; the abdomen is coarsely tuberculate and the tergal sulci on the third through fifth somites are deep. *Sicyonia martini* also differs from *S. affinis* in the barely to distinctly concave (instead of convex) anterior margin of the pleuron of the first somite; the anteroventral extremity of the four anterior pleura which are markedly angular, forming angles of about 90° or less, rather than being rounded or broadly angular; and the outline of the fourth abdominal pleuron which is subpentagonal and often bears a spine on the posteroventral angle, whereas in *S. affinis* it is subcircular and always unarmed.

Sicyonia martini differs further from *S. aliaffinis* by the presence on the first abdominal somite of a short but conspicuous longitudinal ridge extending posteriorly from the ventral end of the anteromedian pleural sulcus. The anteromedian and posteromedian pleural sulci of the second and third abdominal somites are shorter than in *S. aliaffinis*, extending dorsally only to about a third of the height of the somite from the middorsal line rather than to a fourth, and the posteromedian ones are curved anteriorly at their dorsal extremities. Finally, *S. martini* lacks the conspicuous purplish-brown mark (resembling a longitudinally disposed "9" located posterior to the hepatic sulcus and just ventral to the branchiocardiac carina) present in *S. aliaffinis*.

Material.—193 specimens from 41 lots.

For list of records see Pérez Farfante and Boothe 1981.

Sicyonia picta Faxon 1893

Figures 47-52

Sicyonia picta Faxon 1893:210 [syntypes: 4♂ 2♀, MCZ 4639, and 2♂ 2♀, USNM 21172, off Golfo de Panamá (7°40′00″N, 79°17′50″W), 127 fm (232 m), 8 March 1891, *Albatross* stn 3387; 1♂, USNM 21171, off Punta Mariato (7°12′20″N, 80°55′00″W), Panama, 182 fm (333 m), 23 February 1891, *Albatross* stn 3355]. Faxon 1895:180, pl. 46, fig. 2, 2a-c. H. Milne Edwards and Bouvier 1909:244. De Man 1911: 112. Bayer et al. 1970:A97. Arana Espina and Méndez G. 1978:27, fig. 10-13. Brusca 1980:256. Méndez G. 1981:47, pl. 10, Fig. 83-86. Pérez Farfante 1982:372.

Eusicyonia picta. Burkenroad 1934a:95, fig. 35, 1934b:126, 1938:87. Anderson and Lindner 1945:318.

Vernacular names: rock shrimp, target shrimp, Japanese shrimp (United States); cacahuete, camarón de piedra, camarón de roca, camarón japonés (Mexico). FAO names: peanut rock shrimp (English), camarón cacahuete (Spanish), boucot cacahouette (French).

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing one tooth posterior to level of hepatic spine and raised in high, arched crest behind posterior tooth. Abdomen with tooth on dorsomedian carina of first somite conspicuously larger than posterior tooth on carapace. Petasma with distal projection of dorsolateral lobule slightly curved mesially, its compressed tip produced dorsally in strong, hooklike spine. Thelycum with plate of sternite XIV flat or slightly elevated laterally; posterior component of median plate flat or slightly raised laterally. Branchiostegite with ocellus consisting of red center surrounded by yellow ring.

Description.—Body relatively slender (Fig. 47). Carapace sparsely studded with long setae and bearing patches of shorter setae on dorsum; patch also present anteroventral to hepatic sulcus, another elongate obliquely disposed on branchiostegite, and others on lateral depression and anteroventral part of sixth abdominal somite. Abdomen with few small tubercles on first three somites, most on row behind posterior sulci.

Rostrum short, usually not overreaching distal margin of eye, its length increasing linearly with carapace length (Fig. 48), but proportionately longer in young (0.40-0.25 cl); in males (Fig. 49*B*), weakly arched, subhorizontal or upturned, usually not more than 25° but occasionally 30°, deep basally, gently narrowing to slender, short tip (Fig. 49*A*); in females, nearly straight, raised 25°-40°, deep along almost entire length, slightly narrower and truncate apically; in both sexes armed with two to four dorsal teeth and two or three apical

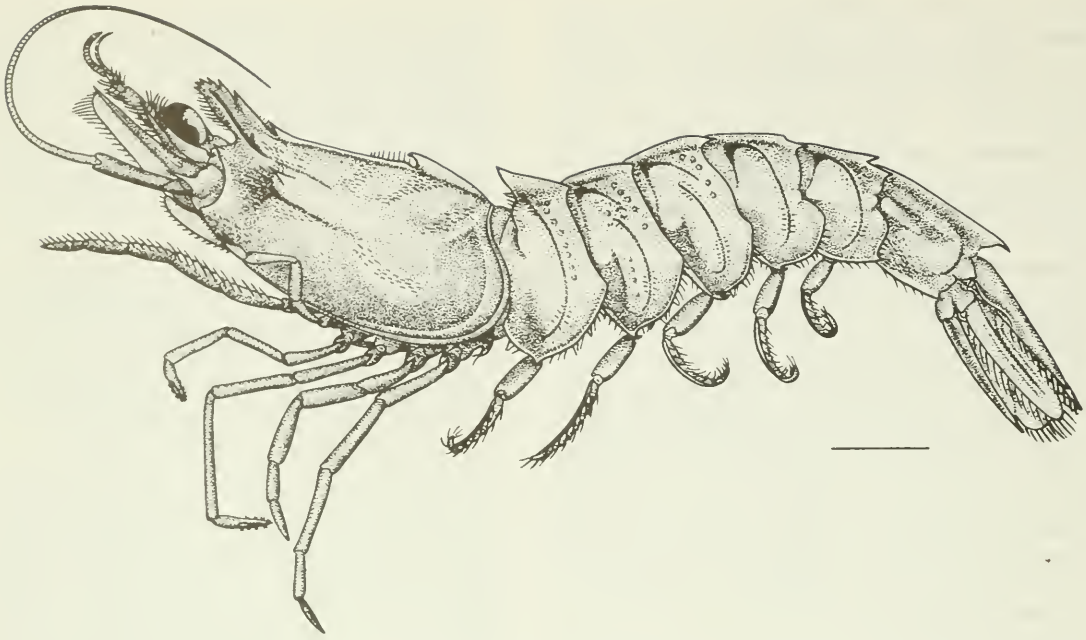


FIGURE 47.—*Sicyonia picta* Faxon 1893. Syntype ♀ 19 mm cl, off Golfo de Panamá. Lateral view. Scale = 5 mm.

ones (3+3, 58%; 4+3, 19%; 4+2, 22%; 3+2, 0.5%; 2+3, 0.5%), dorsal teeth in females often crowded anteriorly with apical ones, about evenly spaced along margin in males. Adrostral carina, subparallel and close to ventral margin, extending to base of apical teeth.

Carapace with well-marked postrostral carina bearing two teeth: 1) epigastric tooth small, subequal to or only slightly larger than first rostral tooth, situated distinctly anterior to hepatic spine, between 0.13 and 0.16 (mean 0.15) cl from orbital margin; and 2) posterior tooth, much larger, four or five times higher, than epigastric, hooklike, its apical portion acutely pointed and strongly curved anteroventrally, situated far posterior to hepatic spine but well in advance of posterior margin of carapace, between 0.60 and 0.68 (mean 0.64) cl from orbital margin. Postrostral carina low anteriorly, slightly elevated just in front of posterior tooth, and forming high crest descending gently from latter to posterior margin of carapace. Tuft of setae present at anterior base of each tooth. Antennal spine sharp, projecting from short, low buttress; hepatic spine considerably larger than antennal, arising from moderately raised area, and situated between 0.18 and 0.24 (mean 0.22) cl from orbital margin. Postocular sulcus deep anteriorly, continuing posteriorly as low groove; hepatic sulcus deep; hepatic carina indistinct; branchiocardiac carina recognizable only posteriorly, extending for short distance subparallel to slope of posterior tooth, then curving dorsally to posterior margin of carapace.

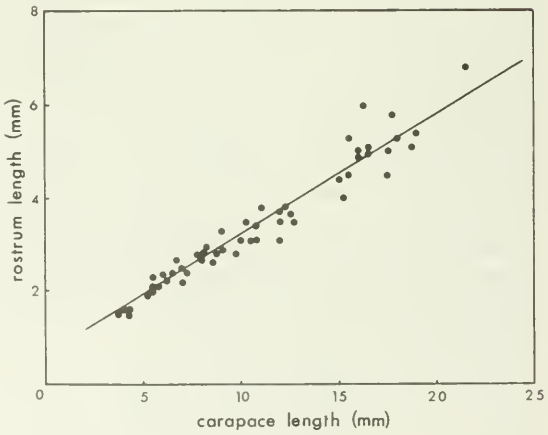


FIGURE 48.—*Sicyonia picta*. Relationship between rostrum length and carapace length (regression equation, $y = 0.51173 + 0.26668x$).

Antennular peduncle with stylocerite produced in long spine, its length 0.75-0.85 distance between lateral base of first antennular article and

mesial base of distolateral spine; latter, slender and sharp, extending to about midlength of second antennular article; antennular flagella short, mesial one slightly shorter, 0.20-0.30 cl, than lateral, 0.25-0.35 cl.

Scaphocerite extending to midlength of third antennular article or slightly overreaching it. Antennal flagellum about twice as much as twice length of carapace.

Third maxilliped slightly stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with dorsomedian carina extending from first through sixth somites, carina on first produced in strong, anterodorsally directed tooth tapering to sharp apex and considerably larger than posterior tooth on carapace; carina on fifth produced in conspicuous sharp tooth and that on sixth terminating in strong, acute one.

Anteroventral margin of pleuron of first abdominal somite concave; posteroventral margin of first through fourth somites rounded; anteroventral extremity of pleuron of first through fourth somites ending in spine, that of first directed ventrolaterally, those of second through fourth curved posterolaterally. Pleuron of fifth and sixth somites bearing posteroventral, caudally directed, relatively small spine, that of fifth slightly larger than that on sixth.

First abdominal somite traversed by anteromedian pleural sulcus, deep dorsally and disappearing at about 0.30 height of somite before reappearing ventrally as broad shallow depression merging with united posterior tergal-posteromedian pleural sulci. Second and third somites with anterior tergal and posterior tergal sulci joining anterodorsally; anteromedian pleural sulcus short (not reaching dorsally posteromedian pleural) but deep and merging with shallow anteroventral depression, latter setting off subelliptical prominence dorsally and low ridge posteriorly; posteromedian pleural sulcus long, extending anterodorsally ventral to (not joining) posterior tergal. Fourth and fifth somites with anterior tergal sulcus and curved, united posterior tergal-posteromedian pleural sulci merging. Sixth somite with arched posteromedian pleural sulcus and longitudinal rib situated along base of middorsal carina and delimited ventrally by deep depression lying just dorsal to weak cicatrix.

Telson with median sulcus deep anteriorly, increasingly shallow posteriorly, its terminal portion elongate and sharp, and bearing pair of small fixed subterminal spines. Rami of uropod subequal in length, falling slightly short of or barely overreaching apex of telson.

Petasma (Fig. 50*A, B*) with rigid distal projection of dorsolateral lobule only slightly curved mesially, raised proximodorsally in rounded prominence and compressed distally, its tip with ventral extremity rounded and dorsal extremity produced in strong, sharp spine directed dorsally. Fleshy distal projection of ventrolateral lobule curving laterally, roughly sickle shaped in outline, with apex directed proximoventrally.

Petasmal endopods coupled in males as small as 6.7 mm cl, about 27 mm tl, but may not be joined in individuals as much as 9 mm cl, about 34 mm tl.

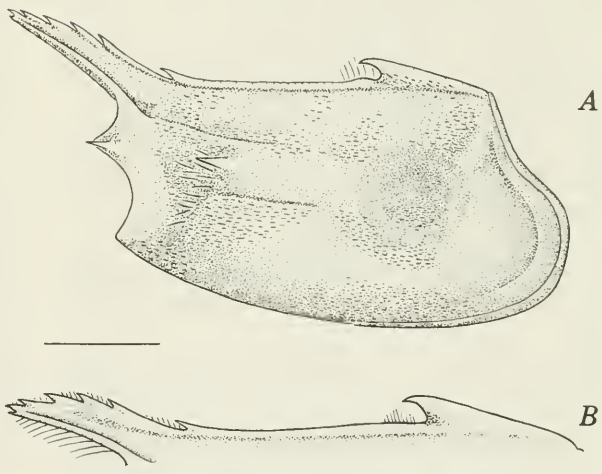


FIGURE 49.—*Sicyonia picta*. *A*, ♂ 16 mm cl, NW of Isla Monserrate, Baja California Sur, Mexico. Lateral view of carapace. Scale = 5 mm. *B*, syntype ♂ 15.5 mm cl. Golfo de Panamá. Lateral view of dorsal part of carapace. Scale = 2 mm.

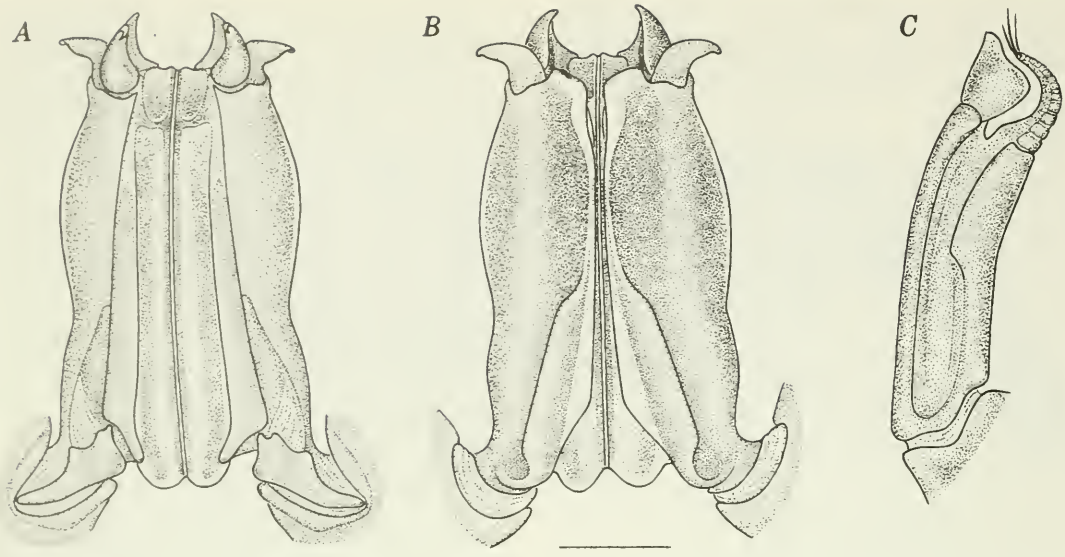


FIGURE 50.—*Sicyonia picta*, syntype ♂ 15.5 mm cl, off Golfo de Panamá. *A*, Petasma dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scales = 1 mm.

Appendix masculina as illustrated in Figure 50*C*.

Thelycum (Fig. 51) with plate of sternite XIV flat or slightly elevated laterally, inclined toward broad median depression, and bordered anteriorly and laterally by narrow, sometimes thickened, flange. Median plate of sternite XIII flask-shaped in outline or subtriangular, tapering anteriorly into long, slender spine reaching between proximal end and midlength of basis of anteriorly extended second pereopods; plate at level of fourth pereopods excavate and constricted by pair of shallow, widely separated lateral incisions; posterior component of median plate, often convex laterally, with rather deep median emargination. Paired short spines projecting from posterior margin of sternite XI. Posterior thoracic ridge narrow, with well-marked anteromedian margin but flush with lateral parts of plate of sternite XIV.

The smallest impregnated females encountered have a carapace of 7 mm, about 28 mm tl.

Color.—Méndez G. (1981) described recently caught specimens as follows: body light red or orange red, with white areas on ventral part of abdominal somites; carapace marked by conspicuous ocellus consisting of red center surrounded by yellow ring. Diffuse dark spot on lateral ramus of

FIGURE 51.—*Sicyonia picta*, syntype ♀ 28 mm cl, off Golfo de Panamá. Thelycum. Scale = 1 mm.

uropod situated distomesially according to her figure 84. Antennae with alternating light and dark red bands. In Formalin, body turns darker red with ring around ocellus, garnet. Faxon (1893, 1895) noted that in specimens preserved in alcohol there is a dark ring on the posterior part of the branchial region and traces of color are present on margins of rostrum, dorsal carinae, and appendages. In most specimens preserved in either agent examined by me, the color pattern described above is still distinguishable.

Maximum size.—Males 17.5 mm cl, about 70 mm tl; females 24 mm cl, 87.9 mm tl (Faxon 1893 and Arana Espina and Méndez G. 1978; corroborated by me).

Geographic and bathymetric ranges.—Bahía Magdalena (24°33′00″N, 112°00′30″W) to southern tip of Baja California Sur, Mexico, throughout the Gulf of California and southward to northeast of Isla María Madre (22°00′N, 106°16′W), Nayarit, Mexico; also from Champerico (13°55′36″N, 92°02′30″W), Guatemala, to Islas Lobos de Afuera (06°45′S, 80°45′W), Peru (Fig. 52). It occurs at depths between 16 and 400 m (shallowest cited by Arana Espina and Méndez G. 1978), but most of the recorded depths are <150 m. It occupies a large variety of bottom types: sand, shell, sand and shell, sand and mud, shell and mud, rock and mud, green, grey and brown mud, broken gravel and shells, and a mixture of mud, rocks, and coralline detritus.

Discussion.—*Sicyonia picta* is most similar to *S. disdorsalis*; both are of moderate size and in addition bear a small epigastric tooth, a large posterior tooth on the postrostral carina, and a strongly developed one on the first abdominal somite. These shrimps can be readily separated by their color pattern and a number of morphological characters. In *S. disdorsalis* an ocellus is lacking on the posterior part of the branchiostegite, the rostrum is slender throughout its entire length, and less elevated than in *S. picta*, its inclination not exceeding 20°; the epigastric and posterior teeth on the postrostral carina are situated closer to the orbital margin, between 0.06 and 0.12 (mean 0.10) cl and 0.55 and 0.65 (mean 0.60) cl, respectively; and the posterior tooth rises from a uniformly low postrostral carina.

The two species also differ in sculpture of the abdomen. In *S. disdorsalis* the first abdominal somite is traversed by a short anteromedian sulcus which is not represented ventrally by a depression; the posterior tergal and posteromedian pleural sulci of the second and third somites are coalescent; the anteroventral extremities of the second through fourth are unarmed or are produced in a small, ventrally projecting spine; and the posteroventral extremities of first through fourth somites are angular, that of the fourth bearing a well-developed spine, and that of the fifth, an extremely long one (instead of small as in *S. picta*) in adults.

In both species the petasma and the thelycum also exhibit distinctive features. In *S. disdorsalis* the distal projection of the distolateral lobule of the petasma terminates in an acute tip rather than being compressed laterally and produced in a

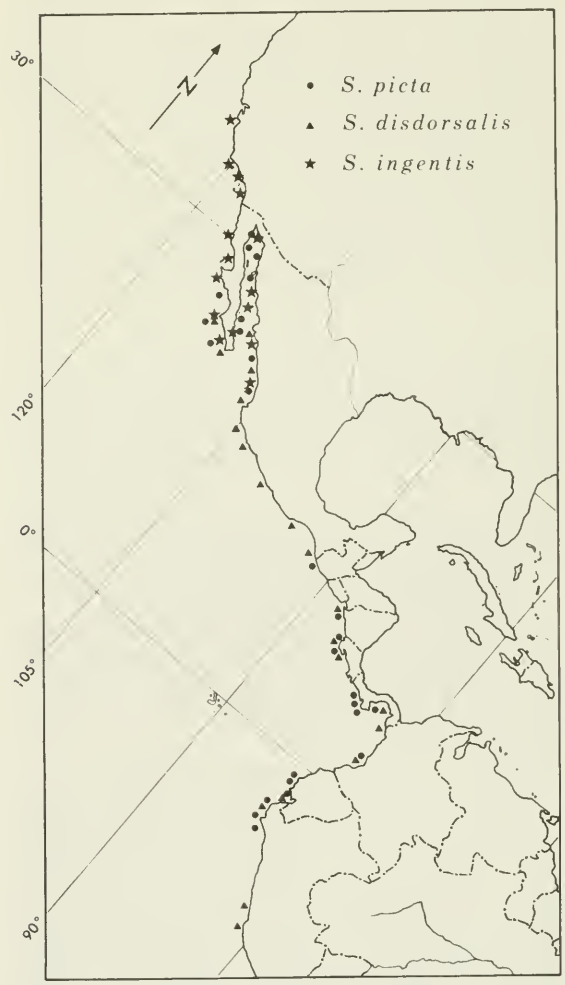


FIGURE 52.—Geographic distribution of *Sicyonia picta*, *S. disdorsalis*, and *S. ingentis*.

dorsally directed salient as it is in *S. picta*. Furthermore, the distal projection of the ventrolateral lobule in *S. disdorsalis* is laminar, bifurcate laterally, and bears a proximal plate bordered by a transverse rib; in *S. picta*, it is roughly sickle shaped in outline, tapering laterally to a sharp proximoventrally directed apex. Finally, the thelycal plate of sternite XIV in *S. disdorsalis* is raised in a low but well-defined pair of lateral protuberances instead of being flat or slightly raised laterally as it is in *S. picta*.

In the field, *S. picta* may be distinguished from its sympatric congeners by the striking yellow ocellus with a red center located on the branchiostegite.

Burkenroad (1938) discussed in detail the features that distinguish *S. picta* from the western Atlantic *S. stimpsoni* Bouvier 1905. Actually, features cited by him for *S. stimpsoni* also apply to *S. burkenroadi*, another western Atlantic species which was not recognized until described by Cobb in 1971. *Sicyonia picta* differs from *S. stimpsoni*, but resembles *S. burkenroadi*, in bearing strongly curved spines on the anteroventral angles of the second through fourth abdominal pleura. It, in turn, can be separated from *S. burkenroadi*, but resembles *S. stimpsoni*, in lacking a posterior tooth on the tergal carina of the fourth abdominal somite.

Remarks.—Arana Espina and Méndez G. (1978) presented an illustration (Fig. 11) in which the posterior tergal and posteromedian sulci of the second and third abdominal somites appear coalescent. The disposition of the posteromedian sulcus seems to be in error because, as stated above, the two sulci in this shrimp do not merge; instead the posteromedian one extends anterodorsally, ventral to the posterior tergal sulcus.

In addition to citing many new localities, this paper contains the first records of the species from the ocean side of Baja California Sur, Mexico, as far north as Bahía Magdalena.

Material.—602 specimens from 61 lots.

Mexico—Baja California Sur: 1♀, AHF, 5.5 km W of mouth of Bahía Magdalena, 64 m, 8 March 1949, *Velero IV*. 1♀, USNM, off Isla Santa Margarita, 86 m, 8 April 1889, *Albatross* stn 3039. 1♂ 2♀, SIO, off Punta Márquez, 64 m, 9 November 1964. 2♀, SIO, Bahía de la Paz, 82-119 m, 12 January 1968, *Thomas Washington*. 2♂ 6♀, SIO, Bahía de la Paz, 119-128 m, 24 July 1965, R. Rosenblatt. 1♂, AHF, entrance to Bahía Agua Verde, 42-48 m, 17 March 1949, *Velero IV*. 6♂ 11♀, SIO, NW of Isla Monserrate, 170-192 m, 11 July 1965, *Horizon*. 2♀, AHF, NW of Isla Danzante Primero, 44-73 m, 18 March 1949, *Velero IV*. 1♂, YPM, Bahía de Santa Inés, 101 m, 17 March 1926, *Pawnee*. 4♀, SIO, off Santa Rosalía, 35-26 m, 25 March 1960, R. Parker. Baja California Norte (all in Gulf of California): 1♀, YPM, Bahía de los Angeles, 31-42 m, 13 May 1926, *Pawnee*. 3♂ 1♀, AHF, Puerto Refugio, Isla Angel de la Guarda, 143-165 m, 28 January 1940. 3♀, AHF, N of Isla Angel de la Guarda, 104 m, 28 January 1940. 6♂ 11♀, SIO, SE of San Felipe, 75-86 m, 19 January 1968, *Washington*. 1♂, YPM, Bahía San Luis Gonzaga, 17 May 1916, *Pawnee*. 1♂ 1♀, USNM, off Punta San Fermín, 55 m, 27 March 1889, *Albatross* stn 3035. 1♀, SIO, SE of San Felipe, 120 m, 19 January 1968, *Washington*. Sonora: 2♂ 2♀, USNM, off Cabo Tepoca, 65 m, 24 March 1889, *Albatross* stn 3018. 26♂ 29♀, USNM, SW of Cabo de Lobos, 139 m, 24 March 1889, *Albatross* stn 3016. 1♂, USNM, NW of Isla Tiburón, 265 m, 24 March 1889, *Albatross* stn 3015. 4♂ 1♀, AHF, 3 km W of Tastiota, 60 m, 21 December 1978, A. Kerotitch. Sinaloa: 3♂ 2♀, USNM, off Punta Santo Domingo, 135 m, 10 April 1889, *Albatross* stn 3043. 1♀, USNM, off Península de Quevedo, 67 m, 30 March 1978, Toral García. Nayarit: 2♂ 4♀, SIO, NE of Isla María Madre, Islas Tres Marías, 82-88 m, 30 March 1973, *Agassiz*.

Guatemala—1♀, SIO, Champerico, 91-104 m, 13 April 1973, *Agassiz*.

Nicaragua—2♀, SIO, off N of Nicaragua, 53-59 m, 17 April 1973, C. Hubbs and S. Luke.

Costa Rica—1♂ 1♀, USNM, Golfo del Papagallo, 2 April 1978, D. Hedgecock. 1♂, SIO, Punta Guiones, 104 m, 19 April 1973, C. Hubbs and S. Luke. 150♂ 150♀, SIO, Golfo de Nicoya, 86 m, 22 April 1973, *Agassiz*. 6♂ 1♀, SIO, off Cabo Blanco, 60 m, 18 April 1973, *Agassiz*. 1♀, UCR, off Cabo Blanco, 249 m, 28 April 1973, *Enriqueta*. 7♂ 14♀, SIO, off Cabo Blanco, 137-144 m, 19 April 1973, C. Hubbs and S. Luke. 1♀, USNM, off Cabo Blanco, 247 m, 27 April 1973, *Enriqueta*.

Panama—1♂ 1♀, AHF, Islas Secas, 46-48 m, 27 March 1939. 2♂ 6♀, AHF, off Isla Medidor, 55-64 m, 28 March 1939, *Velero III*. 2♂ 8♀, UP, 25 km S of Isla Cebaco, 256 m, 8 August 1972, *Canopus*. 1♂, syntype, USNM, off Punta Mariato, 333 m, 23 February 1891, *Albatross* stn 3355. 1♂ 1♀, USNM, E of Isla Iguana, 79-77 m, 2 May 1967, *Pillsbury* stn 502. 3♀, USNM, NE of Isla Iguana, 79-77 m, 4 May 1967, *Pillsbury* stn 515. 4♂ 2♀, MCZ, and 2♂ 2♀, USNM, syntypes,

off Golfo de Panama, 232 m, 8 March 1891, *Albatross* stn 3387. 1♂ 2♀, USNM, S of Isla San José, 84 m, 6 May 1967, *Pillsbury* stn 529. 5♂ 6♀, USNM, S of Isla San José, 99 m, 7 May 1967, *Pillsbury* stn 553. 1♀, USNM, SE of Isla San José, 68 m, 7 May 1967, *Pillsbury* stn 555. 2♂ 3♀, USNM, SE of Isla San José, 60 m, 5 March 1888, *Albatross* stn 2797. 2♂, USNM, S of Isla del Rey, 44-47 m, 7 May 1967, *Pillsbury* stn 551. 1♂ 1♀, USNM, S of Isla del Rey, 59 m, 8 May 1967, *Pillsbury* stn 556. 1♂ 5♀, USNM, SW of Golfo de San Miguel, 64-60 m, 7 May 1967, *Pillsbury* stn 550.

Colombia—Cali: 2♂, USNM, off Bahía de Buenaventura, 80 m, 16 September 1966, *Anton Bruun*, 18B, stn 783.

Ecuador—Manabí: many ♂ and ♀, USNM, off Cabo Pasado, 93 m, 12 September 1966, *Anton Bruun*, 18B, stn 778. 1♂ 3♀, USNM, off Bahía de Manta, 120-150 m, 12 September 1966, *Anton Bruun*, 18B stn 776. 3♂ 3♀, USNM, off Cabo San Lorenzo, 185 m, 12 September 1966, *Anton Bruun*, 18B, stn 775. 1♂ 1♀, AHF, off Isla La Plata, 82-101 m, 10 February 1934. El Oro: 2♂, USNM, SW of Isla Santa Clara, depth unrecorded, 10 September 1966, *Anton Bruun*, 18B, stn 769-D. 27♂ 67♀, USNM, SW of Puerto Bolívar, 80 m, 10 September 1966, *Anton Bruun*, 18B, stn 769.

Peru—Tumbes: 11♂ 8♀, USNM, off Casitas, 90 m, 8 September 1966, *Anton Bruun*, 18B, stn 764. Piura: 4♂ 4♀, USNM, Bahía de Paita, 70-69 m, 8 September 1966, *Anton Bruun*, 18B, stn 762-A. 2♂ 4♀, USNM, Bahía de Paita, 118-133 m, 2 June 1966, *Anton Bruun*, 16, stn 625-A. 1♂, USNM, SW of Isla Foca, 120 m, 7 September 1966, *Anton Bruun*, 18B, stn 761. 4♂ 10♀, USNM, off Punta Negra, 100 m, 4 June 1966, *Anton Bruun*, 16, stn 631-A. Lambayeque: 1♂ 1♀, IMARPE, Islas Lobos de Afuera, 360-400 m, 1977, R. Marquina.

Sicyonia disdorsalis (Burkenroad 1934)

Figures 52-56

Eusicyonia disdorsalis Burkenroad 1934a:96, fig. 25, 36 [syntypes: 1♂ 1♀, YPM 4391, 5♂ 6♀ (not 4♂ 7♀ as originally cited), YPM 5075, and 1♂ 1♀, YPM 4391, Pearl Islands (Archipiélago de las Perlas), 8°29′40″N, 78°52′30″W, Golfo de Panamá, 19-24 fm (35-44 m), 31 March 1926, *Pawnee*; 5♂ 5♀ (not 6♂ 4♀), YPM 5079, and 1♀, YPM 5078, Golfo de Panamá, 1868, F. H. Bradley. 1♂ 3♀, YPM 5076, and 1♂, YPM 5077, west coast of Central America, 1872, Capt. Dow]. Burkenroad 1938:87. Anderson and Lindner 1945:318.

Sicyonia disdorsalis. Chirichigno Fonseca 1970:7, fig. 4. Bayer et al. 1970:A97. Del Solar et al. 1970:18. Rosales Juárez 1976:41, pl. 1, fig. 3. Rodríguez de la Cruz 1977:11. Arana Espina and Méndez G. 1978:29, fig. 14-17. Brusca 1980:256. Paul and Hendrickx 1980: 110. Sosa Hernández et al. 1980:14. Méndez G. 1981:48, pl. 10, fig. 87-90. Pérez Farfante 1982:370.

Vernacular names: rock shrimp (United States); camarón conchiduro (Mexico, Panama); camarón duro (Ecuador, Peru); langostino cáscara dura, camarón cáscara dura (Peru). FAO names: keeled rock shrimp (English), camarón carenado (Spanish), boucot carène (French).

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing one tooth posterior to level of hepatic spine and low throughout its entire length, not raised in crest behind posterior tooth. Abdomen with tooth on dorsomedian carina of first somite considerably larger than posterior tooth on carapace. Petasma with distal projection of dorsolateral lobule curved mesially, tapering to apex, and lacking filament. Thelycum with plate of sternite XIV raised in pair of lateral bulges; posterior component of median plate flat or slightly raised laterally. Branchiostegite lacking large spot or ocellus.

Description.—Body relatively slender (Fig. 53). Carapace bearing patches of short setae on dorsum, anteroventral to hepatic spine, and ventral to hepatic sulcus; patches of setae also present on dorsal extremity of abdominal sulci and in depression of sixth abdominal somite. Abdomen with numerous tubercles on first three somites.

Rostrum relatively short, rarely overreaching eye, its length increasing linearly with carapace length (Fig. 54) to about 18 mm cl, then increasing little, not surpassing 6.2 mm (proportional length decreasing with increasing size from as much as 0.36 to as little as 0.21 cl); slender but occasionally moderately deep; in males subhorizontal with tip strongly decurved, in females upturned as much as 20° with tip slightly decurved; armed with three, occasionally two, dorsal teeth and two or three apical teeth (2+2, 2%, 3+2, 92%, 3+3, 6%);

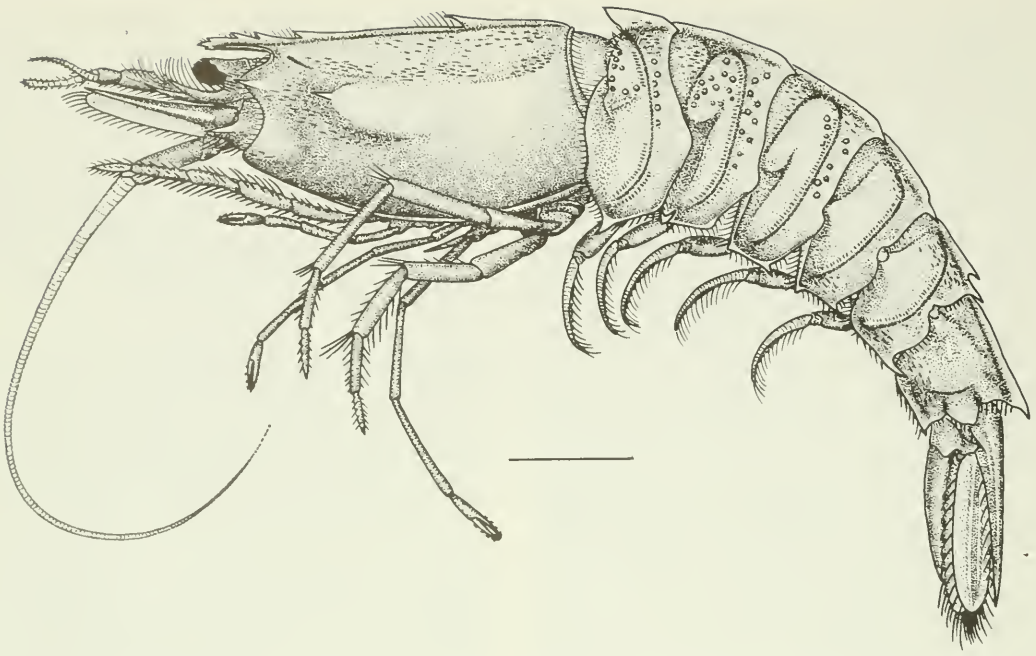


FIGURE 53.—*Sicyonia disdorsalis* (Burkenroad), ♀ 25 mm cl, Golfo de Fonseca, El Salvador. Lateral view. Scale = 10 mm.

ventral apical tooth smaller than dorsal and placed almost at same level or, more often, posterior to it. First rostral tooth located well in advance of orbital margin, between 0.18 and 0.33 (mean 0.25) rl; second tooth from 0.45 to 0.70 (mean 0.58) rl; and third from 0.75 to 0.96 (mean 0.81) rl. Adrostral carina extending to near tip, relatively far from ventral margin, often slightly arched either along middle or less often anteriorly, and occasionally directed anterodorsally.

Carapace with postrostral carina well marked but low throughout its entire length, bearing two teeth: 1) epigastric tooth small, subequal to or slightly larger than first rostral tooth and situated well in advance of hepatic spine, between 0.06 and 0.12 (mean 0.10) cl from orbital margin; and 2) posterior tooth, as large as or larger, sometimes as much as three times higher, than epigastric, acutely pointed, strongly inclined anteriorly, and placed considerably in advance of posterior margin of carapace, between 0.55 and 0.65 (mean 0.60) cl from orbital margin (both teeth farther anterior in large individuals than in young). Tuft of setae present at anterior base of each tooth. Antennal spine moderately long, sharp, buttressed; hepatic spine long, conspicuously larger than antennal, projecting from raised area, and situated between 0.19 and 0.24 (mean 0.22) cl from orbital margin.

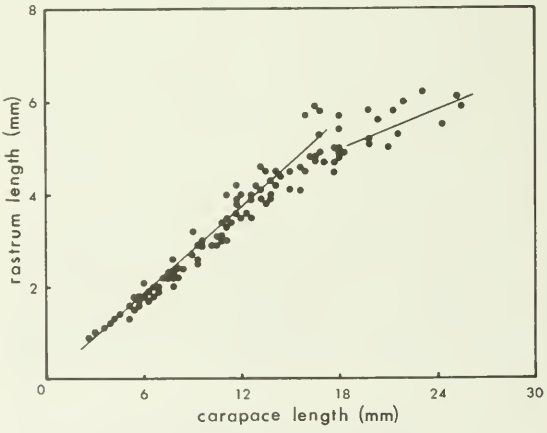


FIGURE 54.—*Sicyonia disdorsalis*. Relationship between rostrum length and carapace length (regression equation for specimens with about 18 mm cl or less, $y = -0.03933 + 0.30998x$; regression equation for those larger, $y = 2.33498 + 0.14502x$).

Postocular sulcus deep anteriorly, continuing posteriorly as very shallow arched groove; hepatic sulcus subhorizontal; hepatic carina indistinct; branchiocardiac carina weak.

Antennular peduncle with stylocerite produced in long, sharp spine, its length 0.75-0.85 distance between lateral base of first antennular article and

mesial base of distolateral spine; latter long, reaching as far as distal 0.25 of second antennular article; antennular flagella short, mesial one, more slender and shorter than lateral, 0.20-0.30 as long as carapace; lateral flagellum 0.25-0.35 as long.

Scaphocerite surpassing antennular peduncle by no more than 0.1 its own length; lateral rib ending distally in long, acute spine conspicuously overreaching margin of lamella. Antennal flagellum about twice as long as carapace.

Third maxilliped stouter than pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with dorsomedian carina extending from first through sixth somites, carina on first produced in strong, anteriorly inclined tooth, tapering suddenly near end to minute, sharp apex (usually broken and thus appearing blunt); tooth considerably larger than posterior one on carapace; carina on fifth somite abruptly truncate or produced in sharp tooth posteriorly, and that on sixth terminating in strong, acute posterior tooth.

Anteroventral margin of pleuron on first abdominal somite concave in adults, sometimes nearly straight in juveniles, its extremity ending in strong spine, that of second through fourth (in adults) often projecting slightly or forming ventrally pointed spine; posteroventral extremity of third through sixth somites sharply angular, that of third often, but in last three always bearing caudally directed spine, that of fifth and sixth largest and smallest, respectively; additional spine occasionally present immediately dorsal to posteroventral one on fourth somite.

First abdominal somite marked with short, deep anteromedian pleural sulcus and long, united posterior tergal-posteromedian pleural sulci; short, longitudinal ridge extending between anteromedian pleural and posterior sulcus. Second and third somites with anterior tergal sulcus joining united posterior tergal-posteromedian pleural sulci dorsally, and with anteromedian pleural sulcus represented by shallow depression setting off elevation at dorsal extremity. Fourth and fifth somites bearing curved, united posterior tergal-posteromedian pleural sulci; sometimes fourth also with faint anterior tergal sulcus. Sixth somite often marked by weak, sometimes indistinct, arched, posteromedian sulcus and bearing conspicuous cicatrix frequently divided in two.

Telson with median sulcus well defined only along anterior 0.65 of its length and armed with pair of minute, fixed, subterminal spines; latter clearly developed in juveniles but vestigial or lacking in adults. Rami of uropod subequal in length, falling slightly short of or barely overreaching apex of telson.

Posterior spine on first abdominal sternite with wide base and usually concave but sometimes straight lateral margins.

Petasma (Fig. 55*A*, *B*) with cornified distal projection of dorsolateral lobule raised in prox-

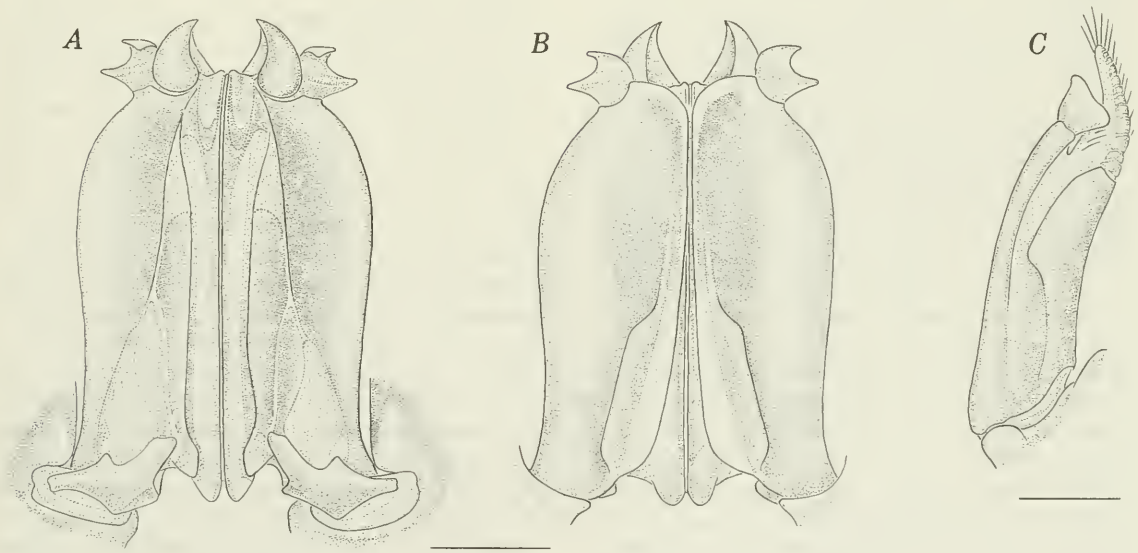


FIGURE 55.—*Sicyonia disdorsalis*, ♂ 17 mm cl, off Balboa, Panama. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scales = 1 mm.

imodorsal rounded prominence and ending in acute tip curved mesially. Distal projection of ventrolateral lobule, falling short of projection of dorsolateral lobule, laminar, bifurcate laterally, and thickened proximally forming plate bordered distally by transverse rib; latter supporting long proximal salient of bifurcation; terminal part of projection truncate and curved dorsally.

Petasmal endopods joined in males as small as 3 mm cl, about 13 mm tl, but may be unjoined in individuals with as much as 8.4 mm cl, about 21 mm tl.

Appendix masculina as illustrated in Figure 55*C*.

Thelycum (Fig. 56) with plate of sternite XIV bearing pair of low protuberances bordered laterally (in adults) by narrow flanges, and separated by moderately deep median depression. Median plate of sternite XIII flask-shaped in outline, tapering into long, slender spine reaching between base and about midlength of basis of extended second pereopod; plate set off from posterior component by shallow incisions, flat or concave posterolaterally, and with broad median depression (broader than areas and incisions flanking it); posterior component of median plate flat or slightly raised laterally, with posteromedian margin straight or convex. Paired short spines projecting anteroventrally from posterior margin of sternite XI, spines broad basally, sharp and sometimes produced in fine needle apically. Posterior thoracic ridge narrow, with well-marked anteromedian margin.

The smallest impregnated females encountered have a carapace of 5.3 mm, about 25 mm tl.

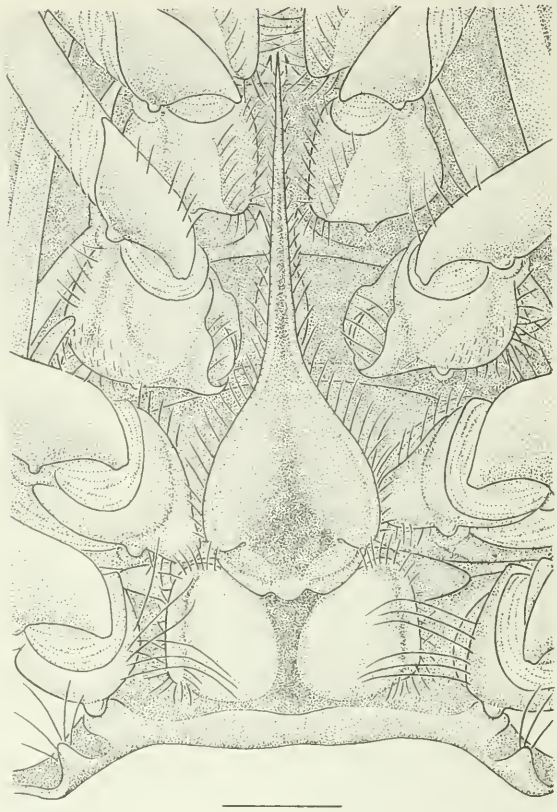


FIGURE 56.—*Sicyonia disdorsalis*, ♀ 16 mm cl, off Punta Calabazo, Panama. Thelycum. Scale = 2 mm.

Color.—Arana Espina and Méndez G. (1978) described specimens from the waters of Peru as follows: Dorsum greenish gray, lighter-gray to pink laterally. Antennae red. Pereopods and pleopods pink; merus of third maxilliped and pereopods with red and yellow bands (toward distal end according to their figure 15). Subdistal striking ornamentation on lateral ramus of uropod consisting of oval deep blue blotch bordered in yellow. In contrast, Sosa Hernándes et al. (1980) found that the specimens from southeast of Salina Cruz, Golfo de Tehuantepec, Mexico, were cream with orange hues.

My observations, based on a large number of live specimens taken off Panamá Viejo, Panama, indicate a color pattern much, but not exactly, like that noted by Arana Espina and Méndez G. Dorsum of carapace gray with broad transverse dark purplish band extending across epigastric tooth and produced anteriorly in roughly pentagonal spot reaching base of first rostral tooth. Branchiostegite varying from dark purplish pink (in most specimens) to milky white, sometimes with grayish white longitudinal stripe along junction of branchiostegite and dorsum. Abdomen gray with middorsal carina banded: transverse dark gray ones alternating with buff bands; large tooth projecting from carina on first somite purplish pink. Anterior margin of pleuron of first three somites bordered by white vertical stripe and posteroventral areas of third and fourth somites also white. Tergum of fifth somite bearing purplish pink V-shaped (vertex anterior) marking posteriorly. Telson and uropod gray with densely set yellow chromatophores. Lateral ramus of uropod bearing large garnet marking subdistally preceded by yellow patch, and contiguous to buff dot lying against its mesial extremity. Antenna dark garnet. Third maxilliped and pereopods pink, former with two contiguous transverse bands, orange red one on

distal third of merus, followed by bright yellow band crossing merus and proximal part of carpus; fourth and fifth pereopods marked with orange red band flanked by yellow ones extending across merus and proximal part of carpus. Pleopods mostly pink, lateroventral part of basis white.

Maximum size.—Males 21 mm cl, 88.8 mm tl; females 28 mm cl, 98.7 mm tl (Arana Espina and Méndez G. 1978). Largest specimens examined by me: males 20 mm cl, females 25.7 mm cl.

Geographic and bathymetric ranges.—Bahía Santa María (24°42′48″N, 112°13′54″W), to the tip of Baja California Sur, Mexico, and from southern Sonora, Gulf of California, southward to Pisco (13°55′S), Peru (Fig. 52).

This species has been found between 5 and 139-93 m, but rarely in water deeper than 65 m; contrary to most of its congeners from the American Pacific, it does not seem to range beyond the continental shelf. It occurs on bottoms of mud, detritus, fine sand, and rock and coral, seemingly with no preference.

Abundant in the southeastern part of the Gulf of California (Paul and Hendrickx 1980), it has not been reported off northern Sonora or along the east coast of Baja California; the present records from these latter areas are the first for the species north of Bahía San Lucas, a locality cited by Burkenroad (1938). The southern limit, Pisco, Peru, given here is also the first report of the presence of this shrimp in waters south of San Lorenzo (12°0.5′S), Peru, the southernmost locality cited by Arana Espina and Méndez G. (1978). The record from Pisco is based on specimens collected by M. Méndez G. and J. Zeballos, at 5.5-13 m, on 5 November 1983 (Matilde Méndez G. footnote 3).

Discussion.—Burkenroad (1938) was the first to point out some of the differences that separate this species from its closest relative *S. ingentis*. *Sicyonia disdorsalis* can be distinguished from the latter by having 1) a sparsely setose carapace, 2) a less elevated postrostral carina, 3) a weak, almost indistinct branchiocardiac carina, 4) a posteriorly truncate carina on the fifth abdominal somite that is sometimes produced in a spine, 5) an anteromedian pleural sulcus on the first abdominal somite which ends abruptly far from the ventral margin, and does not continue ventrally as a shallow depression, 6) a strong spine on the anteroventral extremity of the pleuron of the first abdominal somite, 7) angular posteroventral pleural margins on the first two abdominal somites, 8) minute telsonic spines in juveniles and vestigial or indistinct ones in adults, and 9) short uropodal rami that fall short of or barely surpass the apex of the telson.

Various features of the genitalia also allow the separation of *S. disdorsalis* from *S. ingentis*. The distal projection of the dorsolateral lobule of the petasma is curved distomesially instead of extending distolaterally, and is not produced in a short, apical filament; and the distal projection of the ventrolateral lobule does not extend so far distally as the projection of the dorsolateral lobule, is bifurcate laterally, and bears a conspicuous transverse rib. In the thelycum, the breadth of the flat or concave posterolateral areas of the median plate, as well as the depth of the delimiting incisions are much less than the depressed area between them. Furthermore, the posterior component of the median plate is sometimes slightly raised posterolaterally but not forming well-defined lateral bosses traversed by a suture as in *S. ingentis*.

The differences between *S. disdorsalis* and the geminate western Atlantic *S. dorsalis* Kingsley 1878, were discussed in detail by Burkenroad (1934a).

Commercial importance.—Throughout its range, *S. disdorsalis* is present in the commercial catches of other penaeoid shrimps. It was recorded by Rosales Juárez (1976) in those off the coast of Sinaloa, in the Gulf of California, and more recently, on the basis of its abundance in the shrimp bycatch from the waters off Sinaloa and Nayarit, Paul and Hendrickx (1980) suggested that this shrimp has a possible commercial value in that area. Arana Espina and Méndez G. (1978) recorded that in 1977 it made up to 5.8% of the total catches made in northern Peru, a notable increase from that of previous years in which it constituted <0.5%. This species is considered by them to have a significant economic potential.

Material.—1054 specimens from 85 lots.

Mexico—Baja California Sur: 1♂ 2♀, SIO, Bahía Santa María, 0-37 m, 8 December 1962, H. C. Perkins. 1♂, SIO, NW of Punta Márquez, 37 m, 4 December 1962, H. C. Perkins and R. Wisner. 1♂, SIO, NW of Punta Márquez, 18 m, 4 December 1962, H. C. Perkins. 1♂ 2♀, YPM, Bahía San Lucas, 5.5 m, 7 May 1936, *Zaca* stn 135D-20. 2♂, YPM, Bahía San Lucas, 5-17 m, 7 May 1936, *Zaca* stn 135D-18-D19. Sonora: 7♂ 2♀, USNM, Bahía de Lobos (boca sur), 30 m, 18

July 1979, F. Paredes M. Sinaloa: 27♂ 16♀, SIO, Isla Altamura, 21-31 m, 26 May 1965, *El Golfo II* stn 50-6. 2♀, USNM, off San Ignacio, 25 May 1962, R. Bush M. 1♀, USNM, N of Mazatlán, 3.5 km off Mármol, 12 January 1964, A. Villanía and E. Chávez. 3♂ 8♀, SIO, off Boca Teacapan, 55 m, 25 August 1961, F. H. Berry. Nayarit: 8♀, SIO, W of Laguna de Agua Brava, 20 m, 24 August 1961, H. DeWitt. 2♂ 7♀, SIO, SW of Laguna de Agua Brava, 15 m, 24 August 1961, H. DeWitt and H. C. Perkins. 1♂ 15♀, SIO, NE of Isla María Madre, 51 m, 31 March 1973, *Agassiz*. 2♀, SIO, NW of mouth of Río Grande de Soledad, 38-39 m, 24 August 1961, H. C. Perkins and H. DeWitt. 30♂ 30♀, SIO, Bahía de Banderas, 28-33 m, 2 June 1965, *El Golfo II* stn BT-150. 12♂ 14♀, SIO, Bahía de Banderas, 46-55 m, 21 August 1961, F. H. Berry. 1♂ 1♀, SIO, Bahía de Banderas, 5-9 m, 19 August 1961, F. H. Berry. Jalisco: 2♀, USNM, Puerto Vallarta, 13 April 1937. 11♂ 14♀, SIO, Bahía Chamela, 15-18 m, 2 April 1973, *Agassiz*. 6♂ 15♀, SIO, Bahía Chamela, 27-18 m, 2 April 1973, *Agassiz*. 1♂ 3♀, AHF, Bahía Tenacatita, 4-15 m, 8 May 1939. Michoacán: 1♀, CAS, 14.5 km SE of Punta San Telmo (off Maruata), 17 July 1932, *Zaca*. 7♂ 1♀, SIO, Punta Lizardo, 22-24 m, 4 April 1973, *Agassiz*. 21♂ 25♀, SIO, Punta Lizardo, 37-38 m, 4 April 1973, *Agassiz*. Guerrero: 3♀, CAS, 6.5 km SE of entrance of Bahía de Acapulco, 27 m, 5 April 1932, *Zaca*. Oaxaca: 1♂ 1♀, USNM, 24 km off Puerto Angel, 84-57 m, 13 July 1963, I. Mayés A. 8♂ 4♀, SIO, Golfo de Tehuantepec, 55 m, 6 June 1965, *El Golfo II*, stn BT-162. 5♂ 4♀, SIO, SW of Santiago Astata, 54 m, 6 June 1965, *El Golfo II*, stn BT-162. 1♂ 3♀, USNM, 16 km W of Ayutla lighthouse, 54 m, 15 June 1963, I. Mayés A. 7♂ 30♀, SIO, off Salina Cruz, 44 m, 7 June 1965, *El Golfo II*. 5♀, USNM, Salina Cruz, 64 m, 23 August 1963, I. Mayés A. 4♂ 2♀, SIO, off Salina Cruz, 31-35 m, 8 July 1963, D. Dockins. 1♀, SIO, off Salina Cruz, 49-73 m, 8 July 1963, D. Dockins. 44♂ 50♀, SIO, Golfo de Tehuantepec, 22 m, 10 April 1973, *Agassiz*. 5♂ 5♀, INP, off Tangola, 68 m, 10 July 1963, I. Mayés A. 5♂, USNM, off Tangola, 139-93 m, 13 July 1963, I. Mayés A.

Guatemala—1♀, AHF, San José, 4-9 m, 23 March 1939.

El Salvador—3♂ 8♀, SIO, Golfo de Fonseca, 18 m, 17 April 1973, C. Hubbs and S. Luke. 6♂ 4♀, SIO, Golfo de Fonseca, 18 m, 17 April 1973, C. Hubbs and S. Luke. 5♂ 14♀, SIO, Golfo de Fonseca, 24-29 m, 17 April 1973, *Agassiz*.

Nicaragua—1♂ 5♀, USNM, off northern Nicaragua, 53-59 m, 17 April 1973, C. Hubbs and S. Luke.

Costa Rica—3♀, USNM, 3 km off Río Savegre, Puntarenas, 24 m, 2 December 1981, M. Hatziolos. 10♂ 14♀, SIO, Cabo Blanco, 60 m, 18 April 1973, *Agassiz*. 5♂ 15♀, SIO, Cabo Blanco, 60 m, 18 April 1973, *Agassiz*. 1♂ 2♀, AHF, Golfo de Nicoya, about 1 km of east end of Islas Negritos Afuera, 64 m, 29 June 1973, *Velero* stn 19132. 30♂ 30♀, USNM, Golfo de Nicoya, 31 m, 22 April 1973, C. Hubbs and S. Luke. 40♂ 40♀, SIO, Golfo de Nicoya, 31 m, 22 April 1973, *Agassiz*.

Panama—1♀, USNM, off Bocas del Toro, 91-97 m, 26 January 1971, *Pillsbury* stn 1313. 5♂ 3♀, SIO, Isla Cavada, Islas Secas, 40 m, 23 September 1970, W. Newman, T. Dana, S. Luke. 4♂ 4♀, USNM, S of Río Hato, 17 m, 1/2 May 1967, *Pillsbury* stn 488. 1♀, USNM, Bahía de Parita, 22-18 m, 2 May 1967, *Pillsbury* stn 490. 1♀, USNM, E of Chitré, 20 m, 2 May 1967, *Pillsbury* stn 491. 2♂ 4♀, USNM, E of Chitré, 18-16 m, 2 May 1967, *Pillsbury* stn 492. 6♂ 6♀, USNM, N of Isla Iguana, 37-33 m, 2 May 1967, *Pillsbury* stn 493. 1♂, USNM, southern end of Bahía Limón, 3 m, 23 July 1966, *Pillsbury* stn 449. 5♂ 5♀, USNM, off Punta Calabazo, 20 m, 1 May 1967, *Pillsbury* stn 486. 2♂, USNM, off Río Hato, 15 m, 1 May 1967, *Pillsbury* stn 485. 1♂, USNM, Ensenada de Chame, *Shimada* stn 48. 2♂ 2♀, USNM, S of Isla Bona, 31-26 m, 1 May 1967, *Pillsbury* stn 484. 18♂ 14♀, USNM, E of Punta Chame, 22 m, 1 May 1967, *Pillsbury* stn 483. 2♂ 1♀, USNM, off Balboa, surface, 9/10 May 1967, *Pillsbury* stn 564. 20♂ 20♀, USNM, off Panamá Viejo, 4 m, 23 February 1973, I. Pérez Farfante. 30♂, USNM, off Juan Díaz, 12-22 m, 15 February 1973, *Patricia*. 1♂ 7♀, USNM, Juan Díaz, 5 m, 4 February 1969, L. G. Abele. 1♂ 1♀, USNM, W of Punta Brujas, 18 m, 6 May 1967, *Pillsbury* stn 536. 1♂ 1♀, syntypes, YPM, Archipiélago de las Perlas, 35-44 m, 31 March 1926, *Pawnee*. 5♂ 6♀, syntypes, YPM, Archipiélago de las Perlas, 35-44 m, 31 March 1926, *Pawnee*. 5♂ 5♀, syntypes, YPM, Golfo de Panamá, 1868, F. H. Bradley. 1♀, syntype, YPM, Golfo de Panamá, 1868, F. H. Bradley. 1♂ 3♀, syntypes, YPM, W coast of Central America, 1872, Capt. Dow. 1♂ 3♀, syntypes, YPM, W coast of Central America, 1872, Capt. Dow.

Colombia—1♀, USNM, Bahía Humboldt, 20 April 1967, *Shimada* stn 76B, haul 1. 2♀, USNM, Bahía Humboldt, 20 April 1967, *Shimada* stn 76B haul 2. 6♀, USNM, off Timbiqui, Cauca,

38-35 m, 16 September 1966, *Anton Bruun* 18B stn 785.

Ecuador—1♀, USNM, Golfo de Guayaquil, 32 m, 11 September 1966, *Anton Bruun* 18B stn 772.

Peru—13♂ 22♀, USNM, off Tumbes, 13 m, 10 September 1966, *Anton Bruun* 18B stn 768. 16♀, USNM, off Caleta Cruz, Tumbes, November 1979, *Promaresa*. 16♂, USNM, off Caleta Cruz, Tumbes, November 1979, *Promaresa*. 16♂, USNM, off Caleta Cruz, Tumbes, November 1979, *Promaresa*. 16♀, USNM, off Caleta Cruz, Tumbes, November 1979, *Promaresa*. 6♀, USNM, off Negritos, 16 m, 2 June 1966, *Anton Bruun* 16 stn 624-B. 2♂ 1♀, USNM, Paita, 1969, J. Sánchez and E. Valdivia. 2♀, USNM, NW of Paita, 40 m, 1977.

Sicyonia ingentis (Burkenroad 1938)

Figures 52, 57-60

Eusicyonia ingentis Burkenroad 1938:88, fig. 31-34 [holotype: ♂, AMNH 12388; type-locality: off east coast of Cedros Island (Isla Cedros), 28°05′N, 115°09′W, Baja California, Mexico, 38 fm (69 m), 27 March 1936, *Zaca* stn 127D-1]. Anderson and Lindner 1945:318. Feinberg 1971:6. Frey 1971:16.

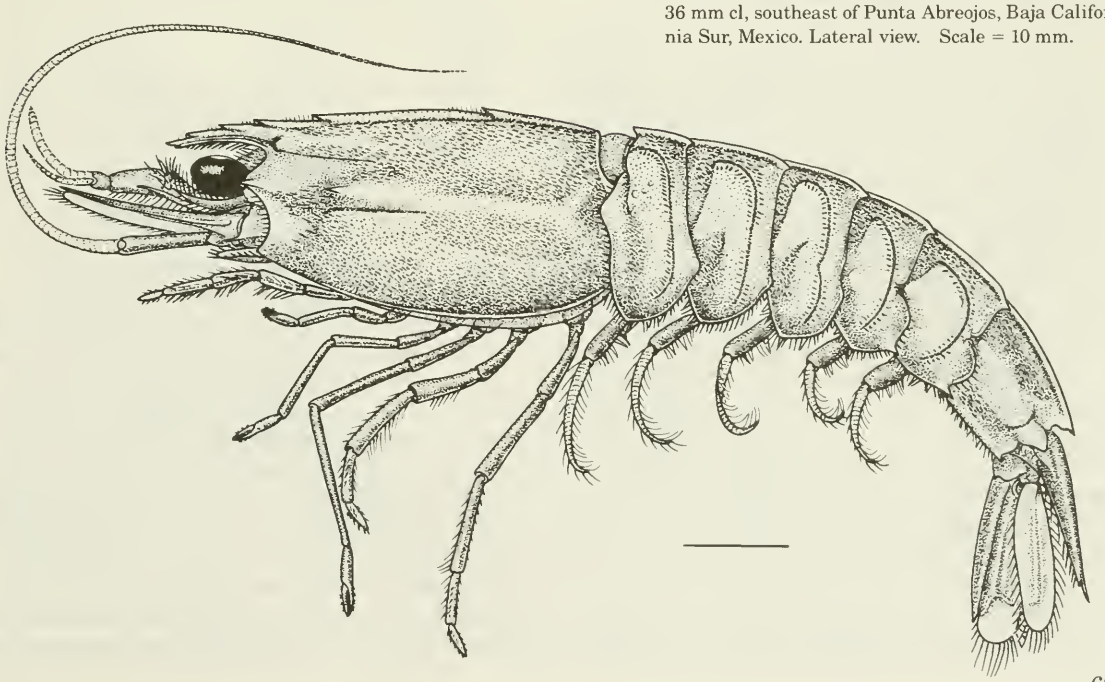
Sicyonia ingentis. Parker 1964:162. Carlisle 1969:239. Longhurst 1970:272. Word and Charwat 1976:19, 3 fig. Holthuis 1980: 61. Wicksten 1980:360. Pérez Farfante and Boothe 1981:424. Pérez Farfante 1982:371. "?Sicyonia sp.", Mathews and González, 1975:51. *Sicyonia ringens*. Mathews, 1981:329.

Vernacular names: ridgeback prawn, rock shrimp, Japanese shrimp (United States); camarón de piedra, cacahuete (Mexico). FAO names: Pacific rock shrimp (English); camarón de piedra del Pacífico (Spanish); boucot du Pacifique (French).

Diagnosis.—Antennal spine well developed and buttressed. Second abdominal somite with dorsomedian carina lacking incision. First pereopod with basis and ischium unarmed. Postrostral carina bearing one tooth posterior to level of hepatic spine and low throughout entire length, not raised in crest behind posterior tooth. Abdomen with tooth on dorsomedian carina of first somite smaller or only slightly larger than posterior tooth on carapace. Petasma with distal projections of dorsolateral lobules divergent and bearing short terminal filament. Thelycum with plate of sternite XIV raised in pair of lateral bulges; posterior component of median plate bearing pair of lateral bosses cut by transverse suture. Branchiostegite lacking large mark.

Description.—Body slender (Fig. 57) and lacking

FIGURE 57.—*Sicyonia ingentis* (Burkenroad 1938), ♀ 36 mm cl, southeast of Punta Abreojos, Baja California Sur, Mexico. Lateral view. Scale = 10 mm.



tubercles or occasionally with few on first abdominal somite. Carapace bearing patches of short setae on dorsum, on pterygostomian and anterior part of branchial regions, bordering branchiocardiac carina, and cluster immediately anteroventral to hepatic spine; patches also present on abdomen flanking dorsomedian carina and on anteroventral part of pleuron of first three and sixth somites. Abdomen lacking tubercles or with few on first somite.

Rostrum slender, usually somewhat decurved but sometimes subhorizontal, occasionally with anterior extremity upturned; moderately long, overreaching distal margin of eye (extending as far as basal 0.2 of second antennular article), its length 0.30-0.43 cl, increasing linearly with carapace length (Fig. 58); armed with three dorsal teeth and two (rarely three) apical teeth, ventral one considerably smaller than dorsal and usually placed posterior to it but occasionally at same level or even more anteriorly; first rostral tooth subequal to, or slightly smaller than epigastric and located opposite and anterior to level of orbital margin, second tooth situated between 0.32 and 0.44 (mean 0.37) rl from orbital margin; and third tooth betwen 0.58 and 0.80 (mean 0.66) rl. Strong adrostral carina, parallel to and rather near ventral margin, extending along entire length of rostrum.

Carapace with postrostral carina low but robust throughout its entire length in adults, weak in juveniles, and bearing two teeth: 1) epigastric tooth small, subequal to or barely larger than first rostral tooth, situated anterior to but relatively near level of hepatic spine, between 0.11 and 0.17 (mean 0.16) cl from orbital margin; and 2) posterior tooth usually slightly, sometimes conspicuously, larger than epigastric and placed well in advance of posterior margin of carapace, between 0.57 and 0.65 (mean 0.63) cl from orbital margin. Tuft of setae present immediately anterior to base of each tooth. Antennal spine moderately long, projecting from sharp, elongate buttress; hepatic spine long, acutely pointed, arising from raised area, and placed between 0.20 and 0.25 (mean 0.22) cl from orbital margin. Postocular sulcus deep anteriorly, continuing posteriorly as long, well-marked arched groove; hepatic sulcus subhorizontal; hepatic carina indistinct; branchiocardiac carina strong, longitudinally disposed but curving dorsally near posterior margin of carapace where also often sending short branch ventrally.

First article of antennular peduncle and gnathal appendages, except third maxilliped, illustrated in Figure 4.

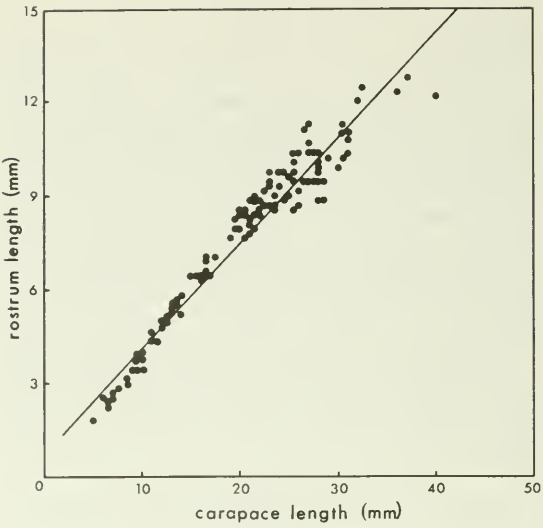


FIGURE 58.—*Sicyonia ingentis*. Relationship between rostrum length and carapace length (regression equation, $y = 0.75763 + 0.33933x$).

Antennular peduncle with stylocerite produced in long, sharp spine, its length 0.85-0.95 distance between lateral base of first antennular article and mesial base of distolateral spine; latter reaching as far as midlength of second antennular article; antennular flagella relatively long, mesial one, about 0.4 as long as carapace, longer and more slender than lateral; latter about 0.30 as long as carapace.

Scaphocerite overreaching antennular peduncle by as much as 0.2 of its own length; lateral rib produced distally in long, acute spine considerably surpassing margin of lamella. Antennal flagellum about 2 times as long as carapace.

Third maxilliped about as slender as pereopods. Basis and ischium of first pereopod unarmed.

Abdomen with dorsomedian carina extending from first through sixth somites, carina on first very low and produced in small, stubby, anterior tooth, smaller or only slightly larger than posterior tooth on carapace; carina on first five somites sloping posteriorly, on sixth produced in large acute posterior tooth.

Anteroventral margin of pleuron of first abdominal somite slightly convex, sometimes straight in juveniles; posteroventral margin, similar to that of second and usually third somites, gently curved. Anteroventral extremity of pleuron of first four somites lacking spine, although that of second and

third occasionally projecting slightly or forming small spine. Posteroventral extremity of pleuron of first and second somites rounded, that of third variably angular (sometimes bearing spine), and that of fourth through sixth produced in caudally directed spine.

First somite marked with short anteromedian pleural sulcus continuing as shallow depression to near ventral margin of pleuron, and long, united, posterior tergal-posteromedian pleural sulci. Second through fourth bearing anterior tergal sulcus (that of fourth weak or sometimes lacking), and united posterior tergat-posteromedian pleural sulci; second and third also bearing shallow depression representing anteromedian pleural sulcus. Fifth somite with almost indistinct anterior tergal and strongly arched, united posterior tergal-posteromedian pleural sulci. Sixth somite with arched posteromedian pleural sulcus barely, if at all, distinct, and bearing well-marked, long cicatrix.

Telson with median sulcus deep basally, fading posteriorly, and armed with small but well-defined, fixed subterminal spines. Rami of uropod subequal in length, exceeding apex of telson by as much as 0.25 of their length.

Posterior spine on first abdominal sternite broadly subtriangular with blunt apex and straight or usually convex, instead of concave, lateral margins.

Petasma (Fig. 59*A*, *B*) with cornified distal projection of dorsolateral lobule directed distolaterally, acutely pointed, ending in short filament, and raised in proximodorsal, subhemispheric prominence. Distal projection of ventrolateral lobule reaching as far as projection of dorsolateral lobule, mostly fleshy, blunt, and produced in small lateral tooth just proximal to midlength.

Petasmal endopods joined in males 10.5 mm cl, about 41 mm tl, but in individuals with carapace of as much as 19 mm, about 70 mm tl, they may not be joined.

Appendix masculina as illustrated in Figure 59*C*.

Thelycum (Fig. 60) with plate of sternite XIV bearing paired strong protuberances bordered laterally by narrow flanges and separated by deep median depression sharply delimiting their posteromesial margins. Median plate of sternite XIII flask-shaped in outline, tapering gradually into long, slender spine reaching between base and midlength of basis of extended second pereopods; plate set off from posterior component by deep incisions and usually raised posterolaterally in paired rounded prominences flanking narrow depression (narrower than prominences); posterior component of median plate bearing paired strong, short bosses separated by deep median depression, each boss cut by transverse suture. Paired short spines projecting anteroventrally from posterior

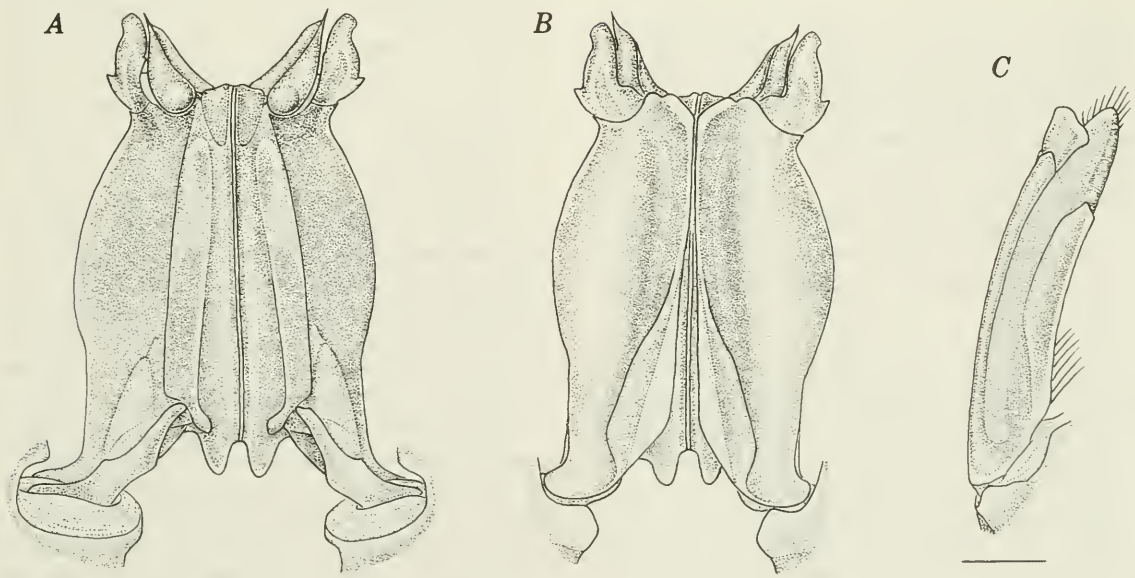


FIGURE 59.—*Sicyonia ingentis*, ♂ 16 mm cl, southeast of Punta Tasco, Isla Santa Margarita, Baja California Sur, Mexico. *A*, Petasma, dorsal view; *B*, ventral view of same; *C*, right appendix masculina, dorsolateral view. Scale = 1 mm.

FIGURE 60.—*Sicyonia ingentis*, ♀ 23 mm cl, southeast of Punta Tasco, Isla Santa Margarita, Baja California Sur, Mexico. Thelycum. Scale = 1 mm.

margin of sternite XI, spines broad basally and sharp or sometimes needlelike apically.

The smallest impregnated females encountered had a carapace of 14 mm, about 57 mm tl.

Maximum size.—Males 157 mm tl; females 180 mm tl, measured from "telson to base of antenna" (Herkelrath 1977). In my sample: males 31 mm cl, about 112 mm tl; females 40.2 mm cl, about 133 mm tl.

Geographic and bathymetric ranges.—Monterey Bay, 36°50'N, 121°50'W (Pérez Farfante and Boothe 1981), California, southward to Isla María Madre, 22°00'N, 106°16'W, Nayarit, Mexico; in the Gulf of California (Fig. 52) along the central part of the eastern coast; and in the southern part along both coasts. This species has been found between 5 and 293-307 m and is most abundant from 55 to 82 m, at which depth it is commercially fished off Ventura, Calif. (Frey 1971); also most of the many specimens examined by me were taken within this range. According to Carlisle (1969) it is common at depths between 61 and 183 m. *Sicyonia ingentis* occurs on substrates of sand, shell, and green mud, but seems to prefer sandy bottoms on which commercial concentrations are located.

This species is the only member of *Sicyonia* that has been recorded along the west coast of the United States and north of Punta Canoas, Baja California Sur—about 1,000 km south of Monterey Bay, the northern limit of its range. The record from Isla María Madre, Nayarit, is the first from waters south of the Gulf of California.

Discussion.—*Sicyonia ingentis*, the largest eastern Pacific species in the genus, has its closest affinities with the much smaller, sympatric *S. disdorsalis*. It differs from the latter in possessing 1) a carapace bearing, not lacking, patches of long setae, 2) a robust postrostral carina rather than a slender one, 3) a strong branchiocardiac carina instead of an almost indistinct one, 4) a carina on the fifth abdominal somite which slopes gently to near the posterior cleft rather than being truncate or produced in a spine, 5) an anteromedian pleural sulcus on the first abdominal somite which continues as a shallow depression almost to the ventral margin of the pleuron instead of ending abruptly and well above it, 6) an unarmed anteroventral extremity on the pleuron of the first abdominal somite rather than one armed with a strong spine, 7) curved, instead of angular, posteroventral pleural margins on the first two abdominal somites, 8) well-developed telsonic spines instead of minute or indistinct ones, and 9) long uropodal rami that considerably surpass the apex of the telson instead of falling short of or barely overreaching it.

Sicyonia ingentis also differs from *S. disdorsalis* in characters of the genitalia. The distal projection of the dorsolateral lobule of the petasma is directed distolaterally instead of curving distomesially and is produced in a short apical filament which is lacking in *S. disdorsalis*. The distal projection of the ventrolateral lobule reaches, instead of falls short of, the terminal margin of the dorsolateral lobule; furthermore, it is neither bifurcate laterally nor does it bear a transverse rib. In the thelycum, the median depression on the posterior part of the median plate of sternite XIII is narrower than the usually rounded protuberances flanking it, whereas in *S. disdorsalis* the depression is much broader than the flat or concave areas which occupy the position of the two protuber-

ances. Finally, the paired lateral bosses, representing the posterior component of the median plate and each cut by a transverse suture, are found only in *S. ingentis*.

The "pencil of hairs" that Burkenroad (1938) stated to be located on the dorsal surface of the distal part of the ocular peduncle, near its distolateral margin, actually is placed on the distomesial margin. He distinguished *S. ingentis* from *S. disdorsalis* by, among other characters, the relative length of that tuft of setae, stating that in large adults of the former species it overreaches the eye whereas in *S. disdorsalis* it spans no more than half the cornea. This character does not seem to be a reliable one for, except in occasional specimens of *S. ingentis*, in neither species does the tuft surpass the eye. Burkenroad also considered the disposition of the adrostral rib as a diagnostic feature that would serve to separate the two species. Although in *S. ingentis* the rib lies parallel to the ventral margin of the rostrum, in *S. disdorsalis* its course varies: sometimes it is slightly arched near the anterior end, as Burkenroad described it, but often it is curved along the middle and occasionally is slightly turned anterodorsally. The distance of the rib from the ventral margin in the two shrimps, however, exhibits a slight difference—in *S. ingentis* it extends close to the margin whereas in *S. disdorsalis* it lies more dorsally.

The characters exhibited by *S. ingentis*, *S. disdorsalis*, and *S. picta* suggest that they must have diverged quite early from a common ancestor in the group of species that share two teeth on the postrostral carina.

Notes on biology.—Herkelrath (1977) investigated the temperature tolerance and age-growth and length-weight relationships in this shrimp. He found that within a salinity range of 33-35‰ it exhibits a wide range of tolerance to temperature (4°-30°C). At a stressed salinity (26‰) this tolerance was considerably reduced (7°-25°), and mortality increased proportionately with the duration of exposure, regardless of temperature. His studies indicated that shrimp with a total length of 50-90 mm increased 10 mm per month and also that there is no difference in length-weight ratio between sexes. He also stated that among shrimp "averaging 70 mm or greater in total length, the average length of females was greater than that of males."

Anderson (1983) studied growth rates, molting, and certain aspects of reproduction in a population of *S. ingentis* occurring off Santa Barbara, CA. She found that spawning takes place far offshore in deep water, about 145 m, and lasts from May through October with the peak during the late summer. She also observed that molt frequency is highest in the winter and spring, that females do not molt during the summer (the reproductive period), and that males exhibit a similar pattern. Size-frequency analyses based on monthly offshore and nearshore sampling indicated that juveniles increased at a monthly rate of about 1-2 mo.

Commercial importance.—There is a fishery for this shrimp between Santa Barbara and Ventura, Calif. According to the California Department of Fish and Game, landings in 1982 amounted to 127,000,956 lb with a value of $156,000,385. Mathews (1981) stated that "*Sicyonia ringens*" is occasionally fished in Magdalena Bay, which is located on the ocean side of Baja California Sur. I have little doubt that his remark applies to *S. ingentis* and that "*ringens*" is an erroneous spelling. Moreover, it seems to me almost certain that the study of "Sicyonia sp." (distribution, abundance, rate of growth, ratio total weight/total length) in Magdalena Bay by Mathew and González (1975), was based on a population of this species, apparently the only abundant rock shrimp in the area. However, because Magdalena Bay is within the range of *S. penicillata*, another species reaching sizes reported by the authors, it is not possible to be certain of the identity of the shrimp studied by them. It is indeed unfortunate that the valuable information presented cannot be definitely associated with a specific shrimp, particularly in view of the fact that so little is known of the biology of any of the eastern Pacific rock shrimps. Although *S. ingentis* is present in the Gulf of California, it is not commercially exploited there.

Material.—946 specimens from 52 lots.

United States—California: 1♀, CAS, 2 km W of Moss Landing, Monterey Bay, 50 m, 23 September 1978, D. D. Chivers. 1♂ 3♀, AHF, 5 km off Point Mugu, 40-59 m, 25 April 1976, *Velero IV* stn 24833. 1♂, AHF, 8.4 km W of Venice, 70-73 m, 22 July 1958, J. L. Baxter. 1♀, SIO, SW of Santa Monica Bay, 22 March 1962, F. H. Berry and H. C. Perkins. 3♀, SIO, San Pedro Bay, 27 m, 20 March 1964, U.S. Fish and Wildlife Service staff. 1♂ 4♂, SIO, N of Dana Point, 53-48 m, 29 March 1974, *Agassiz*. 31♂ 20♀, SIO, off San Onofre, 54 m, 29 March 1974, *Agassiz*. 2♂ 2♀, SIO, off San Onofre,

91 m, 29 March 1974, *Agassiz*. 11♂ 15♀, SIO, off Encinitas, 51 m, 29 March 1974, *Agassiz*.

Mexico—Baja California Norte: 7♂ 5♀, SIO, off Bahía de San Quintín, 57 m, 1 April 1962, Fish and Wildlife Service staff. 15♂ 11♀, SIO, off Bahía de San Quintín, 73 m, 4 December 1960, C. Boyd and D. Dockins. 12♂ 10♀, SIO, off Bahía de San Quintín, 74-77 m, H. C. Perkins. 6♂ 6♀, SIO, off Bahía de San Quintín, 143-148 m, 1 April 1962, H. C. Perkins. 2♂ 5♀, SIO, SE of San Felipe, 120 m, 19 January 1968, *Thomas Washington*. 1♀, SIO, W of Punta Prieta, 23 March 1960, H. C. Perkins. 6♂ 7♀, SIO, Bahía Sebastián Vizcaíno, 88 m, 19 August 1960, W. D. Clarke. 1♀, YPM, E of Isla Cedros, 110 m, 22 May 1936, *Zaca* stn 126D-10. 4♂ 1♀, SIO, between San Benito and Isla Cedros, 247-265 m, 27 May 1971, C. Hubbs and S. Luke. 4♂, YPM, E of Isla Cedros, 80 m, 27 March 1936, *Zaca* stn 125D-1. 24♂ 21♀, USNM, E of Isla Cedros, 80 m, 5 May 1888, *Albatross* stn 2838. 12♂ 19♀, SIO, WSW of Red Rock, Bahía Sebastián Vizcaíno, 113-119 m, 25 November 1961, F. H. Berry. 1♂, YPM, E of Isla Cedros, 73 m, 22 May 1936, *Zaca* stn 126D-4. 4♂ 6♀, YPM, E of Isla Cedros, 69 m, 27 March 1936, *Zaca* stn 126D-2. ♂ holotype, AMNH, off east coast of Isla Cedros, 69 m, 27 March 1936, *Zaca* stn 127D-1. 3♂ 1♀ and 2♂ 2♀ paratypes, AMNH and YPM, respectively, collected with holotype. 3♂ 1♀, YPM, E of Isla Cedros, 70-110 m, 27 March 1936, *Zaca* stn 125D-1. Baja California Sur: 3♂ 1♀, SIO, Bahía Sebastián Vizcaíno, 55 m, 11 August 1952, K. S. Norris. 2♂ 2♀, SIO, Bahía de San Cristóbal, 83-87 m, 2 December 1961, F. H. Berry. 19♂ 17♀, SIO, Bahía Asunción, 68-64 m, 17 November 1964, *Black Douglas*. 20♂ 20♀, SIO, SW of Punta San Hipólito, 6 March 1954, "J.M. and W.H." 13♂ 20♀, SIO, SE of Punta Abreojos, 55-59 m, 17 November 1964, *Black Douglas*. 4♂ 17♀, SIO, SE of Punta Abreojos, 73-79 m, 17 November 1964, *Black Douglas*. 27♂ 21♀, SIO, SE of Punta Abreojos, 91 m, 2 December 1960, C. Boyd and D. Dockins. 20♂ 20♀, SIO, WSW of Punta Pequeña, 68-73 m, 16 November 1964, *Black Douglas*. 2♂ 3♀, SIO, 15 km WSW of Boca de las Animas, 55-57 m, 16 November 1964, *Black Douglas*. 14♂ 6♀, SIO, SW of Santo Domingo del Pacífico, 100 m, 20 April 1969. 19♂ 11♀, SIO, 16 km NW of Isla Magdalena, 99-102 m, 16 November 1964, *Black Douglas*. 23♂ 22♀, SIO, off Bahía Magdalena, 88 m, 3 February 1964, C. Hubbs. 30♂ 30♀, SIO, SW of Isla Santa Margarita, 75-81 m, 13 November 1964, *Black Douglas*. 44♂ 26♀, SIT, SE of Punta Tasco, Isla Santa Margarita, 102-106 m, 27 June 1965, *Horizon*. 25♂ 25♀, SIO, W of Inocentes, 91-93 m, 10 November 1964, *Black Douglas*. 2♀, SIO, WNW of Punta Lobos, 183-201 m, 9 November 1964, *Black Douglas*. 1♂, SIO, Bahía de la Paz, 82-119 m, 12 January 1968, *Thomas Washington*. Sonora: 1♂ 1♀, SIO, off Hermosillo coast, 289-304 m, 25 March 1960, Curray and R. H. Parker. 1♀, AHF, S of Isla Tiburón, 4-29 m, 25 January 1940. 15♂ 11♀, SIO, off Santa Rosalía, 64-48 m, 25 March 1960, R. H. Parker. 25♂ 25♀, SIO, off Isla San Pedro Mártir, 293-307 m, 21 January 1968, *Thomas Washington*. 1♀, AHF, Bahía de Guaymas, 5 m, 23 March 1949. Sinaloa: 2♂ 1♀, USNM, Puerto de la Punta Altata, 9 May 1962, R. E. Bush. 1♀, USNM, Los Cocos, 42 m, 18 May 1962, R. E. Bush. Nayarit: 24♂ 21♀, SIO, NE of Isla María Madre, Islas Tres Marías, 82-88 m, 30 March 1973, *Agassiz*.

ACKNOWLEDGMENTS

Many persons have assisted me throughout the course of this study. Because of the large area covered I was dependent upon many sources for specimens. I am deeply indebted to the following who have lent collections to me, many of which included materials representing new locality records and range extensions: Dustin D. Chivers, California Academy of Sciences; Enrique M. Del Solar, Instituto del Mar del Perú; Harold S. Feinberg, American Museum of Natural History; Jacques Forest, Muséum National d'Histoire Naturelle, Paris; H. E. Gruner, Zoologisches Museum, Humboldt-Universität, Berlin; Janet Haig, Allan Hancock Foundation, University of Southern California; Willard D. Hartman, Peabody Museum of Natural History, Yale University; Leslie W. Knapp, Smithsonian Oceanographic Sorting Center, Smithsonian Institution; Herbert V. Levi and Catharine G. Sibble, Museum of Comparative Zoology, Harvard University; Spencer R. Luke, Scripps Institution of Oceanography; Juan B. del Rosario, Universidad de Panamá; and Mary K. Wicksten, Texas A & M University, formerly of Allan Hancock Foundation.

I have the privilege of drawing on the considerable knowledge of decapod crustaceans systematics of Horton H. Hobbs, Jr., of the Smithsonian Institution, who has given me numerous suggestions during the investigation and has criticized the manuscript. Fenner A. Chace, Jr., of the Smithsonian Institution, and Bruce B. Collette and Austin B. Williams, both of the Systematics

Laboratory, National Marine Fisheries Service, also have read the manuscript and made helpful comments. I acknowledge their assistance with deep appreciation. I am deeply grateful to Matilde Méndez G., Instituto del Mar del Perú, and to Concepción Rodríguez de la Cruz, Instituto de Pesca, Mexico, for the loan of specimens and for invaluable information concerning materials deposited in their respective institutions. Thanks are also extended to Meredith L. Jones, Smithsonian Institution, whose interest and efforts facilitated my field work in Panama; and for making available critical bibliographic references to Lipke B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden; Alexander Dragovich, Southeast Fisheries Center, National Marine Fisheries Service; and to Michel E. Hendrickx, Instituto de Ciencias del Mar y Limnología, Estación Mazatlán, Mexico.

I wish to thank Billy B. Boothe, Jr., who sorted and identified the *Sicyonia* that had been collected among large quantities of penaeoids from the region under investigation and assisted me with the morphometric work. Joseph L. Russo, formerly of the NMFS Systematics Laboratory, helped with statistical analyses and computer work, and Ruth Gibbons also assisted in the analyses and prepared the graphs and distribution maps. María M. Diéguez applied her artistic talent to the preparation of all of the illustrations except Figures 3, 4, and 7 which were ably rendered by Keiko H. Moore. Finally, I also acknowledge with gratitude the assistance of Arleen S. McClain and Virginia R. Thomas, who patiently typed several drafts of the manuscript.

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VARIABILITY IN DIMENSIONS OF SALMONID OTOLITH NUCLEI: IMPLICATIONS FOR STOCK IDENTIFICATION AND MICROSTRUCTURE INTERPRETATION

JOHN D. NEILSON,[1] GLEN H. GEEN,[2] AND BRIAN CHAN[3]

ABSTRACT

Sagittal otoliths in rainbow trout, *Salmo gairdneri*, and chinook salmon, *Oncorhynchus tshawytscha*, arise by fusion of otolith precursors (primordia) before hatching. Size of the otolith nucleus exhibited considerable variability even in the progeny of a single female. Otolith nucleus length was directly related to the number and position of the primordia and water temperature at which the eggs were incubated. This variability limits the utility of nucleus dimensions as criteria for separating sympatric populations of juvenile steelhead and rainbow trout. Variability in otolith nucleus dimensions also accounted for a significant error in otolith size-fish size relationships in recently hatched alevins.

The early development of otoliths is poorly understood considering their potential use in stock identification (Postuma 1974; Rybock et al. 1975) and in the provision of data on fish age and growth to the daily level of precision (Pannella 1971; Wilson and Larkin 1982). Variability of otolith nucleus size and shape is of particular concern in stock identification studies since nucleus dimensions may be racial characteristics. Rybock et al. (1975) have suggested a positive correlation of the rainbow trout, *Salmo gairdneri*, otolith nucleus size and the mean egg size of the female which, in turn, is positively correlated to the size of the female. Their data on Deschutes River steelhead trout (the sea-run form of *S. gairdneri*) females, which were larger, on average, than females of the sympatric population of freshwater resident rainbow trout, led to the suggestion that otolith nucleus dimensions would differ significantly and provide a basis for racial identification of juveniles. This hypothesis was of particular significance since no other meristic or morphometric trait is known which permits identification of juvenile sea-run and freshwater resident *S. gairdneri*.

Nucleus dimensions might affect the widths of concentrically formed daily growth increments deposited around the otolith nucleus. Bipartite daily growth increments consist of alternating protein and calcium rich zones (Brothers 1981), and their widths are proportional to fish growth during the period of increment formation (Wilson and Larkin 1982). If increment width and number vary as a function of nucleus size and shape, then a source of the 15% error described by Wilson and Larkin in the estimation of fish growth from otolith growth could be identified.

In this paper, we describe development of sagittal otoliths of *S. gairdneri* (sea-run and freshwater resident) and chinook salmon, *Oncorhynchus tshawytscha*, and examine the effect of water temperature on otolith nucleus dimensions. These data permit a reexamination of the hypothesis of Rybock et al. (1975). Finally, the implications of variability in otolith nucleus size on otolith microstructure and its interpretation are considered.

METHODS

To study otolith nucleus development in *S. gairdneri*, we obtained eggs from steelhead trout in the Deadman River, British Columbia (B.C.), in 1981 and from the Nicola and Deadman Rivers in 1982 (Thompson River tributaries). Rainbow trout eggs were taken from the Deadman River in 1981, and from stocks in Mission Creek and Pennask Lake in south-central B.C. in 1982. Prior to fertilization, samples of eggs ($n = 20$) were taken for dry weight determination (17 of 18 fish collected in 1982). In all cases, eggs were fertilized with pooled sperm from 2 to 3 males of similar size and origin as the female. In total, eggs from 10 steelhead and 11 rainbow trout were used in this study.

[1]Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6; present address: Marine Fish Division, Canada Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B., Canada E0G 2X0.
[2]Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6.
[3]British Columbia Fish and Wildlife Branch, Ministry of Environment, Kamloops, B.C., Canada V2C 5Z5.

Manuscript accepted April 1984.
FISHERY BULLETIN: VOL. 83, NO. 1, 1985.

The fertilized eggs of each female were incubated in separate compartments in Heath Trays at Abbotsford and Loon Lake trout hatcheries. In 1981, fertilized eggs from two female steelhead and one female rainbow trout were subdivided into three lots and held at 6.5°, 9.5°, and 15.0°C until yolk-sac absorption. In 1982, all fish were held at 11°C. An approximate 12:12 LD photoperiod was maintained through incubation and rearing. Samples of steelhead and rainbow trout eggs or alevins were taken at biweekly intervals in 1981. Alevins only were sampled in 1982.

Oncorhynchus tshawytscha eggs were taken from the 1981 Capilano River stock and were incubated at 6°C under an approximate 12:12 LD photoperiod. Hatchery practice did not allow separate rearing of groups of eggs from individual females.

Otolith development in *S. gairdneri* embryos was studied by dissecting the embryo from the egg, clearing it with carbol xylol, and then squashing the embryo between two microscope slides. This treatment, which made noncalcified tissue transparent and amorphous compared with otoliths and other hard parts, permitted otolith examination with a transmitted light microscope at 400×. While we also examined embryos with X-ray and xeroradiographic techniques, satisfactory results were obtained more simply with the carbol xylol treatment.

Examination of the nuclei of otoliths from alevins required that otoliths be ground and polished following the method of Neilson and Geen (1981). The extent of the otolith nucleus in both embryos and alevins was delimited by the first growth increment encircling all central otolith precursors or primordia (Fig. 1). The first growth increment encircling the central primordia generally appeared dark when viewed with a transmitted light microscope. The only primordium outside the nucleus was in the anterior-ventral quadrant and was associated with the formation of the rostrum, the pointed anterior extremity of the otolith shown in Figure 1.

To avoid bias, otolith nucleus length was measured from coded preparations with an ocular

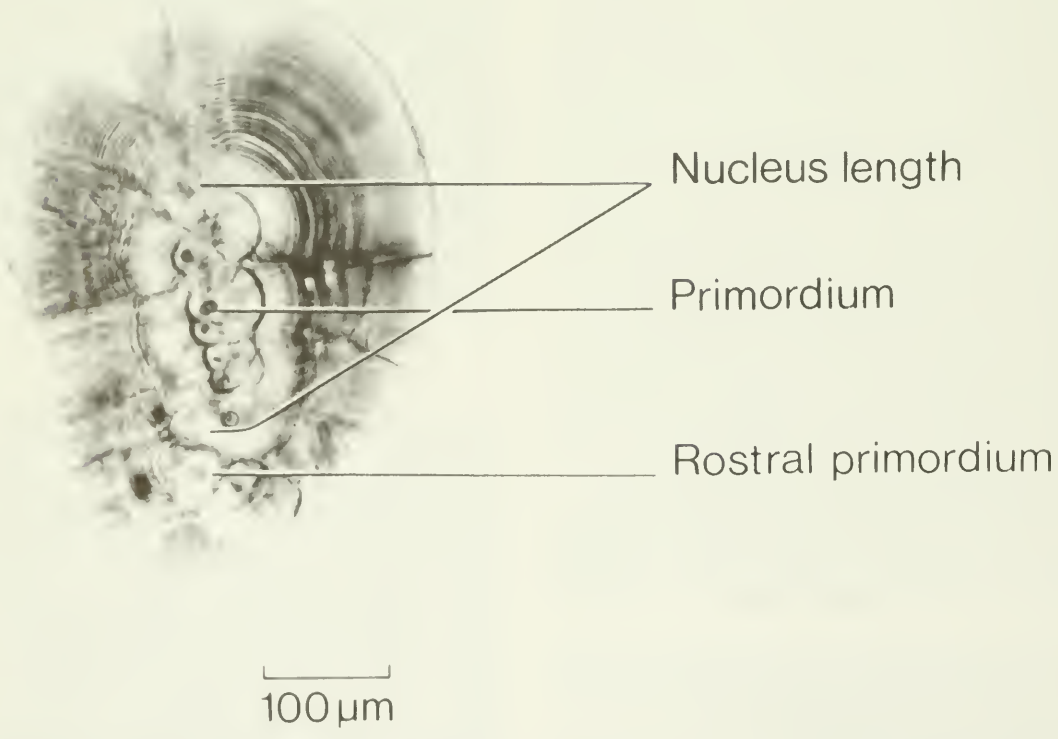

FIGURE 1.—Sagittal otolith from a Capilano River chinook salmon, *Oncorhynchus tshawytscha*, alevin showing the otolith nucleus, primordia, and rostral primordium.

micrometer along the longest axis through the nuclear zone. The area of the otolith nucleus was measured from photographic enlargements with a polar planimeter. Increment widths were measured with a vernier caliper from photographic enlargements (final magnification 9700×). The frequency of increment formation was determined from slopes of regressions of increment counts from otoliths of fish of known age.

Nucleus measurements and primordia counts are only reported for otoliths removed from the fishes' left side as nucleus lengths were significantly greater in left-side than right-side sagittae, albeit at a low level of significance ($P < 0.10$, Wilcoxon Paired Sample Test).

During the course of this study, otoliths from 257 rainbow trout, 187 steelhead trout, and 50 *O. tshawytscha* were examined.

RESULTS

To examine the hypothesis that egg size (a function of female fork length) influences otolith nucleus length in progeny, we examined the relationship of female fork length to egg dry weight and nucleus length in *S. gairdneri*. The dry weight of steelhead and rainbow trout eggs was positively correlated with the size of the female from which the eggs originated ($r^2 = 0.54$, $P < 0.001$, Fig. 2). The slope of the geometric mean regression shown

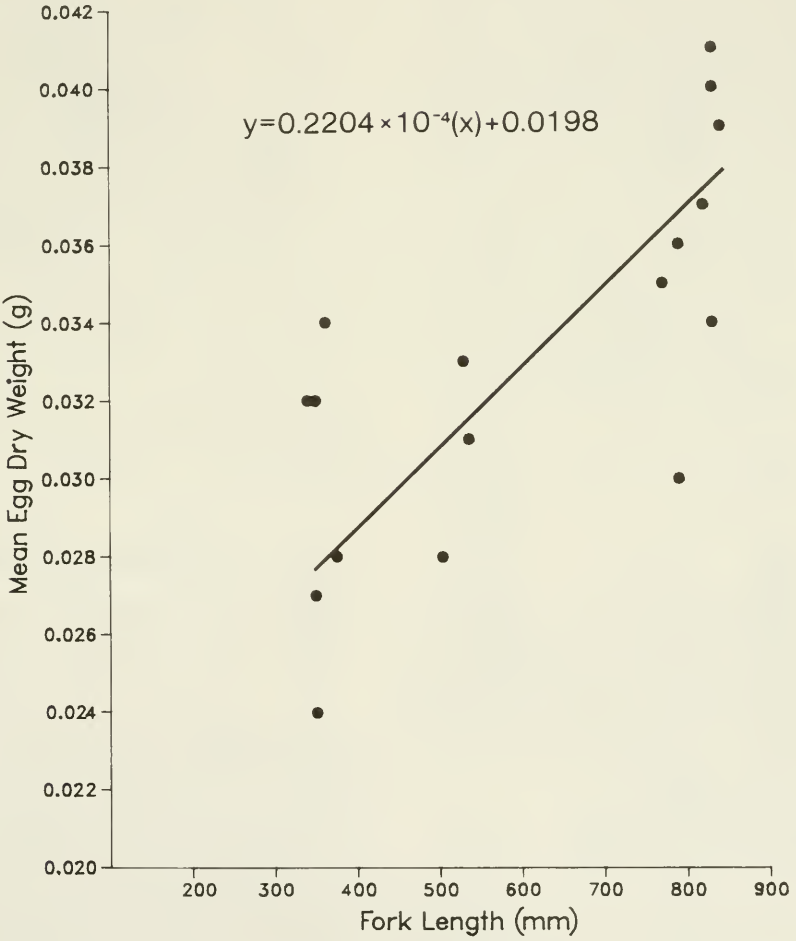

FIGURE 2.—Geometric mean regression of mean unfertilized egg dry weight on fork length of female *Salmo gairdneri* from which eggs were obtained. Each point is the mean of 20 eggs from each female. Fish in the 300-400 mm size interval were rainbow trout from Pennask Lake, those 500-600 mm were rainbow trout from Mission Creek, and those >700 mm were Deadman or Nicola River steelhead.

in Figure 2 differed significantly from zero (t-test, $P < 0.001$). However, there was no significant relationship between otolith nucleus length and female fork length (t-test, $P > 0.05$, Fig. 3), or egg dry weight (t-test, $P > 0.10$). We also investigated the utility of otolith nucleus lengths as a racial characteristic by calculating D^2, a part of a discriminant function analysis. In this instance, D^2 is a measure of the power of discrimination of nucleus length in separating juvenile sea-run and freshwater *S. gairdneri*. D^2 was 0.063 and was not significant ($P > 0.1$).

A major source of the variability in the otolith nucleus length-female parent length relationship (Fig. 3) was apparently related to the ontogeny of otolith nuclei in the salmonid embryos. Otolith nuclei result from the fusion of primordia. Primordia, the first calcified structures to arise in *S. gairdneri* during embryonic development, appeared at 115-214 Centigrade degree-days. Individual primordia increase in size by concentric accretions, ultimately fusing with neighboring primordia to form the nucleus of the otolith at 226-241 degree-days (Fig. 4). Hatching occurred at about 320 degree-days. The pattern of nucleus development was similar in both rainbow and steelhead trout. Although we did not follow otolith development in *O. tshawytscha*, examination of their nuclei suggested that they also arose from fusion of multiple primordia. Deposition of growth increments commenced immediately after fusion.

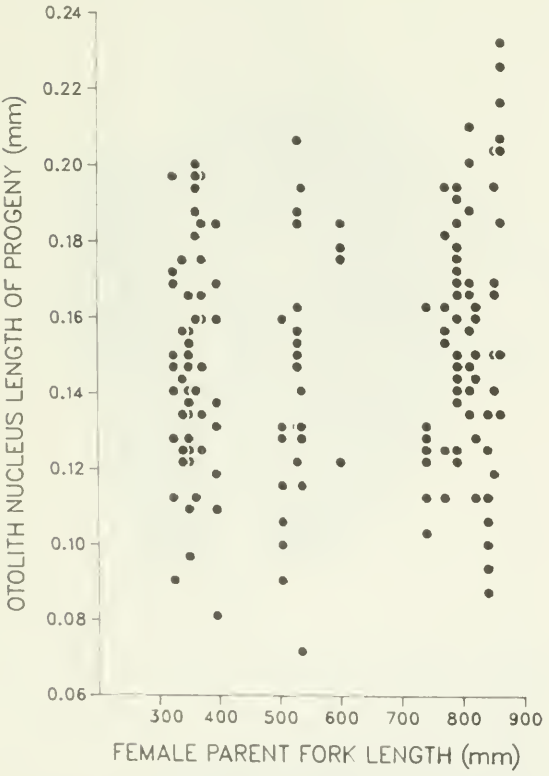

FIGURE 3.—Scatter plot of *Salmo gairdneri* female parent size on otolith nucleus length of progeny. The origin of the adults is given in the caption of Figure 2.

The number of primordia fusing to form the otolith nucleus in the salmonid species we examined was variable, even within the progeny of a single female. In rainbow trout, there was an average of 8.2 ± 2.7 primordia (±1 standard deviation indicated). In steelhead trout and *O. tshawytscha* numbers of primordia averaged 10.7 ± 2.4 and 10.1 ± 2.7, respectively. There were no significant differences in mean primordia counts among the three stocks of rainbow trout or the two stocks of steelhead trout examined (analysis of variance, $P > 0.05$). Figure 5 shows the relationship between the number of primordia deposited and otolith nucleus length.

The variable location of primordia within the nucleus also affects nuclear dimensions and further increases variability. In some instances (<5%), primordia were formed at the periphery of the nucleus, resulting in a local distortion of otherwise regular growth increments (Fig. 6).

Otolith nucleus length (mm) ±1 SE in *S. gairdneri* from the Deadman River was also affected by incubation temperature as shown below:

	Water temperature		
	6.5°C	9.5°C	15.0°C
	----------Mean nucleus length (mm)----------		
Rainbow trout	0.142 ± 0.009	0.174 ± 0.009	0.172 ± 0.008
Steelhead trout	0.154 ± 0.004	0.197 ± 0.008	0.191 ± 0.005

One-way analysis of variance and the Student-Newman-Keuls test indicated that the mean otolith nucleus length in rainbow or steelhead trout reared at 6.5°C was significantly less ($P < 0.01$) than at 9.5° or 15.0°C, although no significant differences in otolith nucleus length ($P > 0.05$) existed in fish reared at the two higher temperatures. The number of primordia formed in both Deadman River steelhead and rainbow trout was independent of the water temperature at which the eggs and alevins were incubated (analysis of variance, $P > 0.05$).

FIGURE 4.—Deadman River steelhead trout sagittal primordia before fusion (right, 214 degree-days) and after fusion (left, 331 degree-days). Bar = 10 μm.

We determined the effect of nucleus size variation on otolith size by examining correlations between nucleus area and otolith area at several stages of development of steelhead trout and *O. tshawytscha* of similar size. We chose to report nucleus area in this case, as it reflects nucleus dimension more precisely than one-dimensional measurements such as nucleus length. While nucleus area and length are significantly correlated ($P < 0.001$), nucleus length accounted for only 47 and 52% of the variability in nucleus area in steelhead trout and *O. tshawytscha*, respectively. The best correlations between nucleus area and subsequent otolith area were noted in relatively small otoliths of recently hatched alevins. The greatest degree of variability in otolith area occurred up to 15 d after nucleus formation (Table 1).

TABLE 1.—Coefficients of variability in otolith area at several stages of development, and coefficients of determination for regressions of otolith area at several stages of development. N = 15 for both steelhead trout and *Oncorhynchus tshawytscha*. The steelhead trout were 29-30 mm FL, and *O. tshawytscha* 30-31 mm. Trout were reared at 9.5°C and *O. tshawytscha* at 6°C.

	Steelhead trout		*O. tshawytscha*	
Stage of otolith development	Coefficient of variation in otolith area (%)	Coefficient of determination (r^2) when regressed on nucleus area	Coefficient of variation in otolith area (%)	Coefficient of determination (r^2) when regressed on nucleus area
Otolith area at nucleus formation	33	n/a	23	n/a
Otolith area 15 d after nucleus formation	15	0.41**	14	0.62**
Otolith area 35 d after nucleus formation	6	0.21 NS	10	0.21 NS
Otolith area 50 d after nucleus formation	7	0.16 NS	11	0.15 NS

** = $P \leq 0.01$.
NS = not significant ($P > 0.05$).

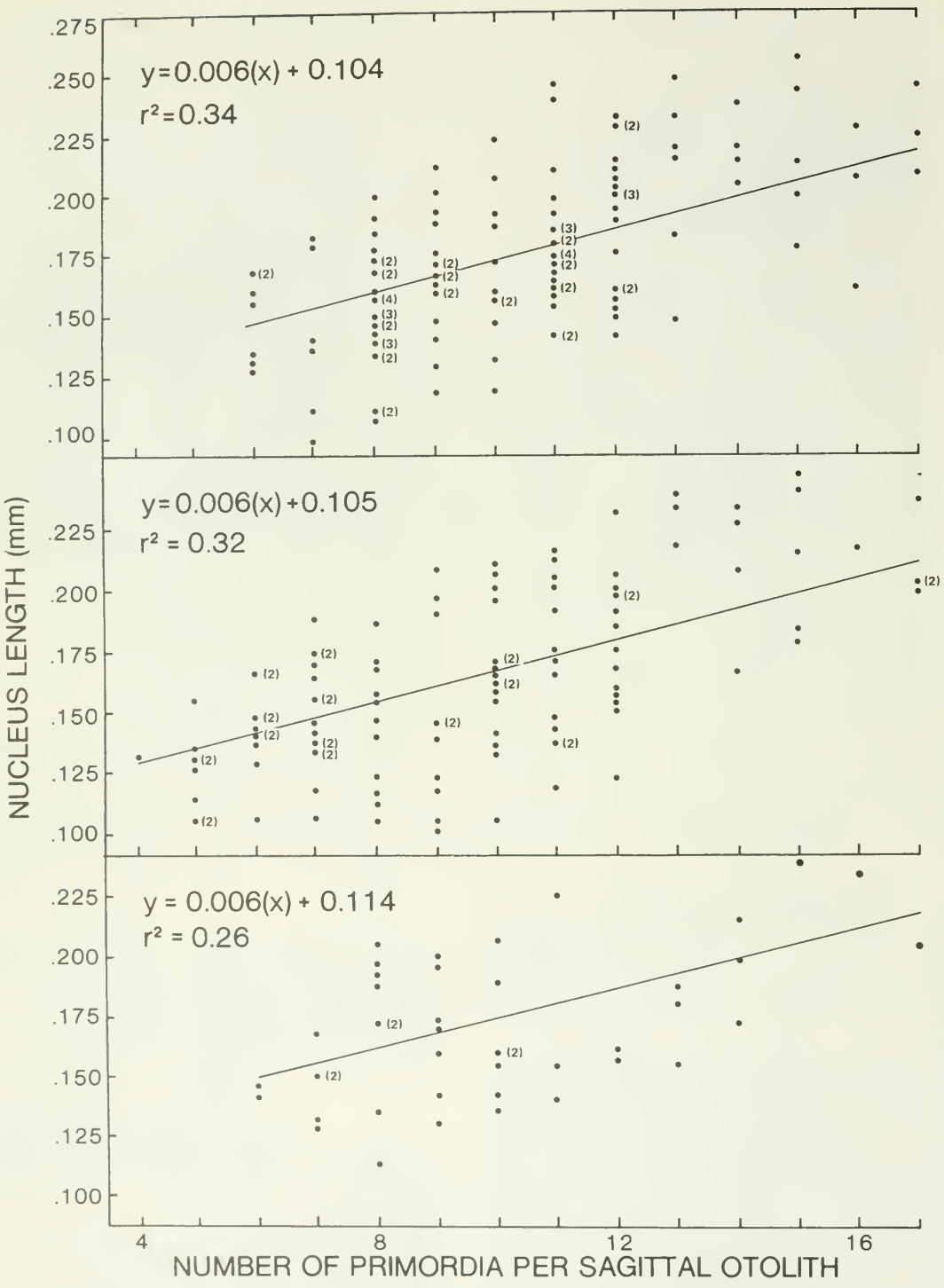

FIGURE 5.—Geometric mean regressions of number of primordia per sagittal otolith on otolith nucleus length for steelhead trout (top), rainbow trout (middle), and Capilano River *Oncorhynchus tshawytscha* (bottom). Trout were incubated at 9.5°C and salmon at 6°C.

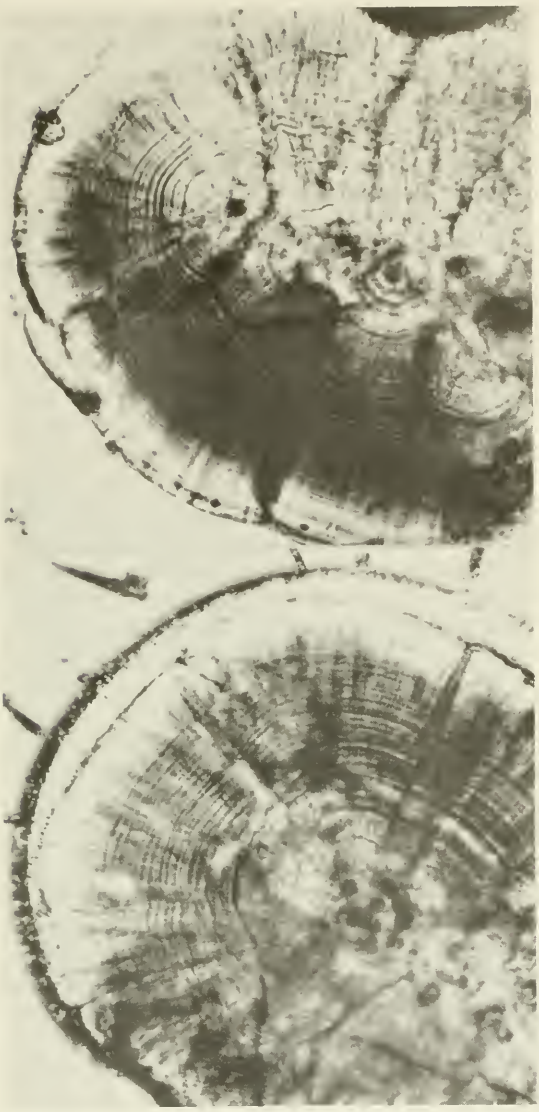

FIGURE 6.—Development of a steelhead trout otolith nucleus resulting from a peripheral primordium (top) and the typical pattern of nucleus development (bottom). Note compression of otolith growth increments in the postrostral quadrant. Otoliths were from progeny of the same female parent.

We did not find any correlation between mean increment width through the various stages of development and nucleus area in either species (t-test, $P > 0.05$). In addition, examination of regressions of increment counts on nucleus area indicated that the frequency of increment formation did not vary as a function of nucleus dimension ($P > 0.10$ for both *S. gairdneri* and *O. tshawytscha*).

DISCUSSION

Sagittal otoliths in *S. gairdneri* embryos arise by fusion of primordia, the first calcified structures to appear during development (McKern et al. 1974). Radtke and Dean (1982) reported similar results for mummichogs, *Fundulus heteroclitus*, and also noted that the otolith nucleus was first apparent as an amorphous gel-like mass in the area of the labyrinth in the developing larvae. Calcified primordia appeared later although Radtke and Dean did not describe any variability in their number or position.

The number and position of the primordia were variable, even within the progeny of a single female. This variation affected the extent of the otolith nucleus. In addition, we observed that water temperature influenced nucleus size. The observed variation in nucleus size limits the utility of this feature as a criterion for stock identification. However, differences in nucleus size did not affect the number of growth increments subsequently formed and had no significant influence on their width.

In our studies eggs were fertilized with the pooled sperm of several males. It is possible that the observed variability in otolith nucleus size was related to the differences between the male parents. There was little difference in the size of the males used, either within the group or relative to the females. We cannot rule out genetic differences between males as a factor affecting variability in nucleus size. However, any genetic effects influencing our results would be no greater than would be expected in natural populations. The numbers of males from which sperm was pooled was usually three, a number frequently involved in fertilization of eggs of a single female in nature (Schroeder 1982; Gross in press).

In developing a hypothesis to explain the basis for use of otolith nucleus length as a means of distinguishing races, Rybock et al. (1975) suggested that nucleus length was related to egg size, although no data were presented. While we found that greater nucleus lengths were associated with larger eggs on average, and larger eggs originated from larger female parents, the slope of the regression of nucleus length on egg weight was not significant (Fig. 3). Furthermore, the variability of otolith nucleus dimensions in rainbow and steelhead trout from south-central B.C. made their measurement much less useful for stock identification that has been suggested for *S. gairdneri* from the Deschutes River, Oreg. (Rybock

et al. 1975). However, otolith nucleus dimensions did serve to separate summer and winter races of steelhead trout (McKern et al. 1974). Workers proposing to use otolith nucleus dimensions as stock identification criteria should consider rearing fish under controlled conditions to establish the extent of nucleus size variability in the stocks in question.

Otolith nucleus length is also influenced by water temperature during embryonic development. Our data showed an increase of about 25% in length in fish reared at 9.5° or 15°C relative to that observed in fish incubated at 6.5°C. The sensitivity of otolith nucleus length to water temperature may allow separation of selected fish stocks whose eggs are incubated at different water temperatures. For example, *O. tshawytscha* juveniles originating from Campbell River stock reared in the Canada Department of Fisheries and Oceans Quinsam Hatchery on Campbell River had significantly greater otolith nucleus lengths ($P < 0.01$) than wild Campbell River *O. tshawytscha* incubated in cooler waters (M. Bradford pers. commun.[4]). Increased water temperature may influence nucleus length through a greater rate of accretion of the calcium/protein matrix around primordia, reflecting a faster rate of embryonic development.

The definition of otolith nucleus suggested here can be consistently applied. With relatively simple preparation techniques, otolith nucleus dimensions can be measured from micrographs or by using a light microscope equipped with an ocular micrometer. Previous workers have delimited the otolith nucleus in relation to metamorphic or nuclear checks. Such terms are ill-defined and should be avoided since they imply that otolith checks result from important developmental events. While it seems likely that such events may result in growth interruptions or checks, causal links have not yet been demonstrated.

The imprecise definition of the periphery of the otolith nucleus may reduce the comparability of measured dimensions derived in various studies. While we have defined the nucleus as lying within the first increment surrounding the primordia, several checks occur during early otolith development. Use of one of these checks to define the periphery of the nucleus would result in inconsistency between various investigations. For example, nucleus lengths of steelhead trout used in this study were generally <0.2 mm (Fig. 3). The mean diameter of the otolith nucleus of summer and winter steelhead reported by McKern et al. (1974) were 0.348 and 0.436 mm, respectively. Differences between studies of this magnitude may be racial in nature or may reflect differences in definition of the extent of the nucleus.

Data on variation in primordia number and location have not been reported previously although the existence of primordia was described by Radtke and Dean (1982) in mummichogs. McKern et al. (1974) did not describe primordia in their work involving the otolith nucleus in steelhead trout. Their results were based on the use of X-ray techniques. We were not able to detect primordia using this method.

It is likely that the otoliths of many fish species are formed by fusion of multiple primordia. From our observations, this is apparently the case in all five species of Pacific salmon and the Pacific herring, *Clupea harengus pallasi*. Radtke and Dean (1982) noted multiple primordia in masou salmon, *O. masou*; Arctic char, *Salvelinus alpinus*; brook trout, *S. fontinalis*; and the sculpin, *Cottus nozawa*.

While both steelhead trout and *O. tshawytscha* otolith nucleus areas were variable, otolith areas in older fish (longer than 15 d after primordia fusion) were less so as indicated by the decreasing coefficient of variation of otolith area with increasing age (Table 1). The decreased variation probably reflects the development of otoliths from an indeterminant array of primordia to the otoliths of adult fish, the latter considered a species-specific characteristic (Fitch 1968; Morrow 1979). However, variation in otolith development in the juvenile salmonids studied here do not present difficulties for the interpretation of microstructure as neither the number nor width of growth increments is significantly affected by nucleus size variation.

ACKNOWLEDGMENTS

The cooperation of the staff at British Columbia Department of the Environment fish hatcheries at Abbotsford, Loon Lake, and Summerland is gratefully acknowledged. In particular, we wish to thank John Cartwright, Dennis Graf, Chris Houston, Bob Land, Don Peterson, and Hugh Sparrow for their exceptional support. Eldon Stone of the Canada Department of Fisheries and Oceans Capilano Hatchery provided the chinook salmon used in this study. Mike Bradford suggested calcu-

[4]M. Bradford, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6, pers. commun. November 1983.

lation of the D^2 statistic. Barbara Puselja and Tracey Crawford assisted with otolith preparation and examination. Ron Long, Department of Biological Sciences, Simon Fraser University, prepared the photographs. This work was supported by a Graduate Research Engineering and Technology Award to G. H. Geen from the British Columbia Secretariat of Science, Research and Development, and a Canada Department of Fisheries and Oceans Subvention Grant.

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EFFECTS OF FEEDING REGIMES AND DIEL TEMPERATURE CYCLES ON OTOLITH INCREMENT FORMATION IN JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

JOHN D. NEILSON[1] AND GLEN H. GEEN[2]

ABSTRACT

The effects of constant and diel cyclic water temperature regimes, feeding frequency, fish activity, and ration level on growth increment formation in juvenile chinook salmon, *Oncorhynchus tshawytscha*, are described. Of the variables examined, any event which recurred more than once every 24 hours increased the rate of increment production above 1 increment per 24 hours. The results were consistent with the hypothesis that environmental variables modify the rate of increment formation by altering the periodicity of fish activity. Both water temperature and ration level interacting with water temperature affected otolith increment width, a measure of fish growth, although ration level did not.

To realize the potential of otolith microstructure in detailed age and growth studies of fishes, knowledge of factors influencing otolith growth is required. The principle features of otoliths likely to be used in such studies are the growth increments which are deposited in a concentric fashion around the otolith nucleus. The frequency of deposition (often 1 increment/24 h) and the width of the increments are both affected by environmental conditions (Neilson and Geen 1982).

The growth increments result from accretion of $CaCO^3$ and to a lesser extent, protein (Simkiss 1974). The daily nature of their deposition observed by many workers (Pannella 1971; Brothers et al. 1976; Wilson and Larkin 1982; and others) appears related to a daily rhythm in the relative rates of calcium carbonate and protein deposition (Mugiya et al. 1981). The cyclic deposition of calcium and protein over a 24-h period results in the formation of the bipartite features now referred to as daily growth increments.

The effects of environmental variables on otolith increment formation have been the subject of some controversy. Taubert and Coble (1977) concluded that a 12:12 LD photoperiod was responsible for entraining diel rhythms in the growth of juvenile *Lepomis* and *Tilapia* sp. otoliths. However, juvenile starry flounder, *Platichthys stellatus*, and chinook salmon, *Oncorhynchus tshawytscha*, continued to produce daily growth increments when exposed to constant light (Campana and Neilson 1982; Neilson and Geen 1982). The latter authors presented evidence that feeding frequency affected both increment number and width in *O. tshawytscha*. They also suggested that feeding frequency (or any other environmental variable) was probably not the ultimate factor determining the frequency of otolith increment production. Environmental modulation of endocrine rhythms (Menaker and Binkley 1981) may ultimately control otolith increment periodicity.

Diel cycles in water temperature have received little consideration as an environmental variable potentially affecting increment formation. Brothers (1978) suggested that diel temperature variations were responsible for otolith increment formation in temperate stream-dwelling fish although no data were presented. This gap in our understanding of factors influencing otolith increment production is significant since diel changes in water temperature are a common feature of aquatic environments. In this study we examined the effects of diel water-temperature regimes on formation of otolith growth increments in *O. tshawytscha* alevins and fry. We also present data on the effects of interactions of water-temperature regimes, feeding frequency, and ration level on otolith increment formation in *O. tshawytscha* fry. Finally, we tested the suggestion made earlier (Neilson and Geen 1982) that feeding periodicity (or any other periodic event affecting fish activity) modifies the rate of otolith increment production through changes in fish activity.

[1]Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6; present address: Marine Fish Division, Canada Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B., Canada E0G 2X0.
[2]Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6.

Manuscript accepted February 1984.
FISHERY BULLETIN: VOL. 83, NO. 1, 1985.

METHODS

Alevins

Fish used in the experiments described below originated from the 1981 brood of the Canada Department of Fisheries and Oceans Capilano Hatchery. Eggs were transferred to incubation facilities at Simon Fraser University at the "eyed" stage of development, corresponding to 347 Celsius degree-days. Prior to transfer, the eggs were held under a 12:12 LD photoperiod and at a constant 8°C water temperature. The eggs were held for 5 d in our laboratory at 8.5°C before exposure to diel water-temperature regimes.

Two lots of 100 fish were exposed as eggs and later, as alevins, over a 69-d period to a water-temperature regime whose diel amplitude averaged 2° and 4°C (range 1.8°-2.4° and 3.0°-4.5°C) above a daily average minimum temperature of 8.5°C. These temperatures were similar to those observed in May-June 1981 in the Deadman River, B.C., a stream supporting an *O. tshawytscha* population. All eggs hatched by day 29. Eggs or alevins (n = 10) were sampled at days 19, 40, 55, and 69. On day 39, 20 alevins were transferred from a temperature regime with a 4°C amplitude and 24-h period to a regime with the same temperature amplitude but a 12-h period. A fourth group was held at a constant 8.5°C. The constant water temperature corresponded to that of the cool period of the diel water-temperature regimes.

Sagittal otoliths were removed from preserved fish and prepared following the methods of Neilson and Geen (1981). Otolith sections were examined using a light microscope or scanning electron microscope (SEM) as described in Neilson and Geen (1982).

Fry

Fry used in these experiments were about 90-d-old posthatch and originated from Capilano River hatchery stock. Prior to transfer to 25 l aquaria at Simon Fraser University, fish were held under natural light at a constant 8°C and fed once every 24 h. After transfer to our laboratory, fry were held for 2 wk in flow-through aquaria supplied with aerated and dechlorinated water at 6°C before experiments commenced. During this period the 50 fish in each aquarium were fed to satiation with Oregon Moist Pellets once per 24 h and exposed to a 12:12 LD photoperiod.

Experimental feeding and temperature regimes to which fry were exposed are summarized in Table 1. Amplitude of daily temperature fluctuations was 4°C (range 3.6°-4.4°C) above the average minimum of 6°C. The diel temperature cycle in relation to photoperiod and feeding events is shown in Figure 1. The activity of one group of fish was artificially increased to examine the effects of activity on otolith increment formation. These fish were forced to evade a slowly moving aquarium net for 10-min beginning at 1900 h daily. The induced activity level appeared similar to that associated with feeding. Ration provided to experimental lots of fish was maintained as a constant proportion (4% or 8%) of average fish dry weight by

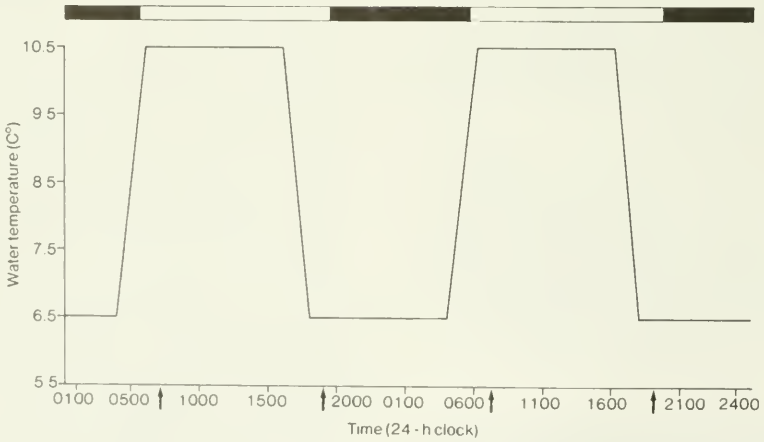

FIGURE 1.—Diel water-temperature cycle in relation to photoperiod and feeding events (↑) for *Oncorhynchus tshawytscha* fry. Light and dark periods are indicated by the open and solid bars respectively.

TABLE 1.—List of abbreviations denoting experimental regimes to which *Oncorhynchus tshawytscha* fry were exposed in 1982. Percent ration (% of body weight offered every 24 h) is given and the water temperature at time of feeding during the diel cycle, if applicable, is indicated in parentheses. Refer to Figure 1 for details of feeding, temperature, and photoperiod regimes.

Treatment	Time of feeding (h)
8% (warm)	0700
8% (cool)	1900
8% (constant)[1]	0700
4% (warm)	0700
4% (cool)	1900
4% (constant)[1]	0700
2 × 4%[2]	0700 and 1900
2 × 2%[2]	0700 and 1900
4% + activity[3]	0700
Starvation	n/a

[1]Fish in these treatments were held at constant temperature.
[2]Fish in these treatments were fed 2 times per 24 h.
[3]Fish in this treatment were held at a constant temperature and exposed to a 10-min bout of forced activity at 1900 h every day.

adjusting total food offered as fish grew or were sampled. Every third day, excess food was removed from the aquaria within 30 min of offering, weighed, and consumption estimated.

On day 26, we exposed fry for 30 min to a hypertonic solution of 1 g/l sodium chloride and 40 mg/l oxytetracycline hydrochloride. The tetracycline was incorporated into the otolith and provided a time marker which exhibited fluorescence when viewed with ultraviolet illumination. All fry were successfully marked by this method.

Originally, we had intended to sample 15 fish at days 10, 20, and 40. However, an accidental interruption of the dechlorinated water supply on day 19 resulted in the mortality of some fish in treatments 4% (cool), 4% (constant), 2 × 4%, and 4% + activity. Complete mortality of starved fish occurred at that time. To ensure an adequate ($N \geq 10$) sample on experiment completion, no samples were taken at day 20 for the above four treatments. Even so, only five fish remained by day 40 in the 4% (cool) treatment.

Fork lengths were determined immediately after the fish were sacrificed. Fish were then dried to a constant weight (60°C for 48 h) in individual labeled containers, and weighed. Sagittal otoliths were then removed, weighed with an electrobalance, and prepared for examination with the SEM or a light microscope.

Increment counts were conducted as described by Neilson and Geen (1982). No attempt was made to distinguish between the daily and subdaily increments as did Brothers (1978) and Campana (1983). Such distinctions are often based on subjective appraisals of increment continuity and appearance when viewed with a light microscope. We did not observe any such differences in growth increments of *O. tshawytscha*. Moreover, as the purpose of this study was to determine the periodicity of increment formation as a basis for detailed study of fish growth, the classification of increments as daily or subdaily was not necessary.

RESULTS

Eggs and Alevins

The formation of growth increments commenced before hatching under all experimental regimes. One increment/24 h was formed on average under all temperature regimes (Table 2). No significant departure from unity was noted (analysis of variance, $P > 0.05$). However, the appearance of the daily growth increments differed between treatments. Otoliths of fish subject to a cycle of temperature were characterized by more regular and easily observed growth increments than those held under constant temperatures (Fig. 2).

Examination with a SEM at 1,000× revealed that the bipartite nature of otolith growth increments differed between the temperature regimes. After etching with a weak acid (Neilson and Geen 1982), the relatively deeply etched portion of the bipartite growth increment (corresponding to the opaque portion of the bipartite structures when viewed with a transmitted light microscope) comprised a larger average fraction of the growth increments ($P < 0.01$) in otoliths of fish subjected to a diel cycle in temperature than those of fish held at constant water temperatures. The lightly etched portion of daily growth increments did not differ significantly between fish held in diel temperature regimes with 2°C and 4°C amplitude (analysis of

TABLE 2.—Summary of *Oncorhynchus tshawytscha* otolith increment counts for alevins held under various temperature regimes.

Experiment day	Increment count[1]		
	Constant temperature	2°C amplitude	4°C amplitude
19	17.8 ± 2.6	18.5 ± 1.2	17.4 ± 1.0
40	—	38.0 ± 2.4	39.5 ± 2.1
55	51.8 ± 2.8	54.1 ± 1.9	53.3 ± 3.0
69	68.4 ± 5.6	68.4 ± 4.1	70.2 ± 4.6

[1]±1 standard deviation indicated, $n = 10$.

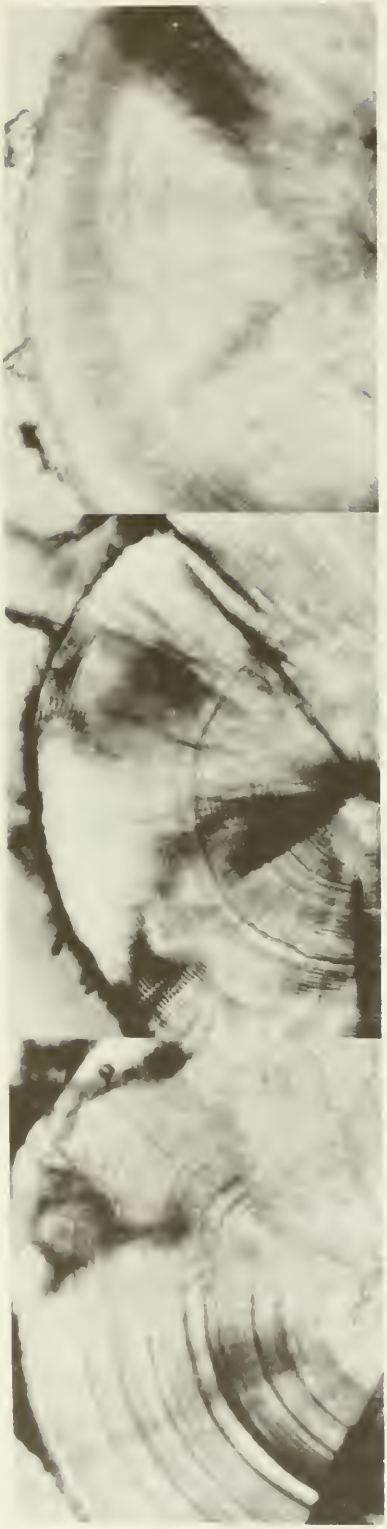

FIGURE 2.—Comparison of *Oncorhynchus tshawytscha* alevin (length 30-31 mm) otolith microstructure in fish held for 60 d in diel water-temperature regimes of 4°C amplitude (right), 2°C amplitude (middle), and constant temperature (left).

variance and the Student-Newman-Keuls test, $P > 0.05$).

Oncorhynchus tshawytscha transferred from a 4°C diel temperature regime (24-h period) to a regime with a 12-h period and similar amplitude produced an average of 1.56 increments/24 h. The slope of the regression of mean increment count on experiment day differed significantly from unity ($P < 0.01$). An example of an otolith from a fish exposed to the 12-h period, cyclic temperature regime is shown in Figure 3 and illustrates the narrower increments associated with the 12-h cycle.

Fry

Otolith growth increments were formed at the rate of one every 24 h in fish fed once per day. No significant departures were noted (t-tests, $n \geq 20$, $P > 0.05$). Fish which received 2 feedings/24 h or 1 feeding and a 10-min bout of activity deposited significantly >1 increment/24 h (t-tests, $P < 0.01$). Arithmetic mean regressions of increment counts on experiment day for the latter treatments are given below:

Treatment	*Regression equation*	r^2
8% B.W. ration fed 2 times/24 h	$y = 1.45(x) + 1.58$	0.91
4% B.W. ration fed 2 times/24 h	$y = 1.76(x) - 1.40$	0.98
4% B.W. ration and forced activity	$y = 1.50(x) - 0.80$	0.93

Slopes of regressions in groups of fish producing >1 increment/d did not differ significantly from each other (analysis of covariance, $P > 0.10$).

The distributions of increment widths in fed groups of fish are presented in Figure 4. A summary of the comparisons of increment width data among treatments is provided in Figure 5. One-way analysis of variance and the Student-Newman-Keuls test indicated that mean increment widths in otoliths of fish receiving a ration of 8% B.W./24 h in one feeding differed significantly between groups ($P < 0.05$). Mean increment widths in otoliths of fish receiving a ration of 4% B.W./24 h in one feeding did not differ significantly in fish receiving the ration either during the cool or warm portion of the diel temperature cycle (Student-Newman-Keuls test, $P > 0.05$). However, fish receiving 4% B.W./24 h under constant water temperature produced growth increments whose mean width was significantly less than those of fish held in the diel water-

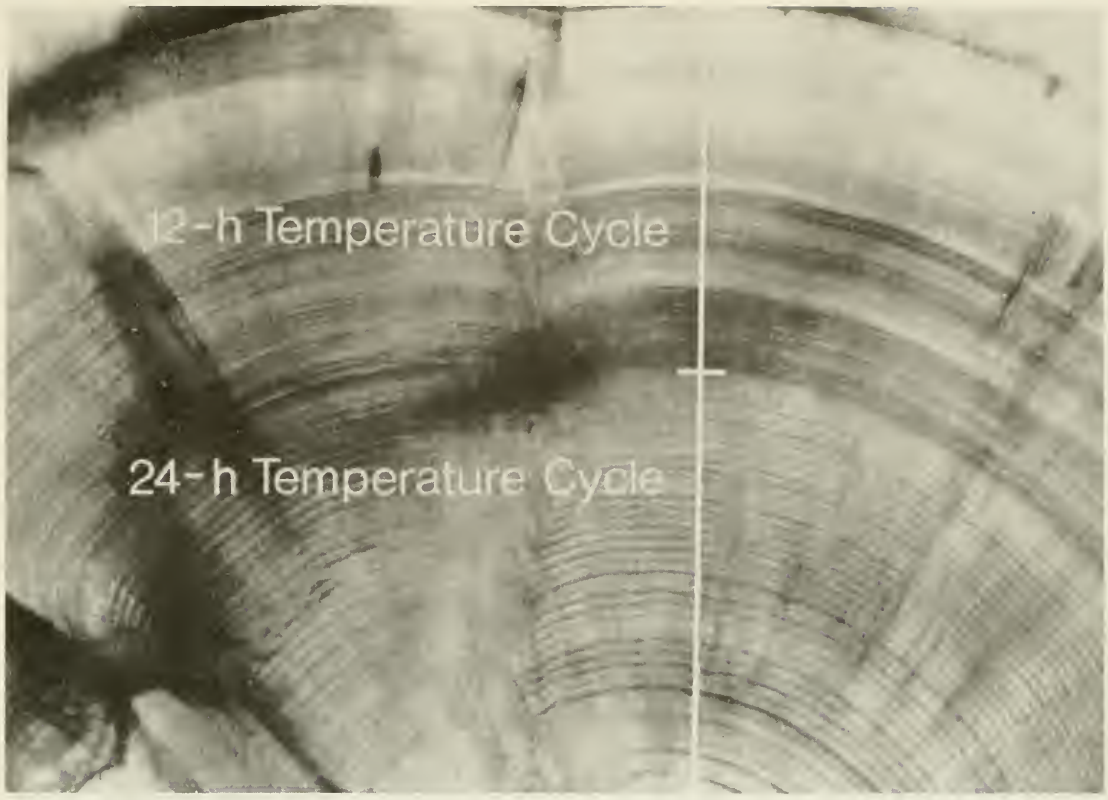

FIGURE 3.—Change in otolith microstructure in a *Oncorhynchus tshawytscha* alevin transferred from a 24-h period temperature cycle (4°C amplitude) to a 12-h period temperature cycle (4°C amplitude).

temperature regimes ($P < 0.05$, Student-Newman-Keuls test).

The top two horizontal strata of Figure 4 constitute a 3 × 2 factorial design and were examined with a two-way analysis of variance. The effects of time of feeding with respect to the diel temperature cycle, ration level, and their interaction were examined in relation to mean otolith increment width. The effect of time of offering with respect to the diel temperature cycle on mean increment width was significant ($P < 0.001$), whereas ration level was not ($P > 0.05$). The interaction of time of offering in relation to the diel temperature cycle and ration level on otolith increment width was also significant ($P < 0.001$).

Fish in treatments receiving 2 feedings/24 h or fed once per 24 h and exposed to a 10-min bout of activity produced growth increments whose average widths were significantly less than those of fish in treatments fed the same ration once per 24 h. Treatments in which fish received either rations of 8% or 4% with 1 or 2 feedings/24 h comprise a 2 × 2 factorial design, and were analyzed with a two-way analysis of variance. Increased feeding frequency significantly reduced mean increment width ($P < 0.001$), although ration level did not ($P > 0.1$). The interaction of feeding frequency and ration level was not significant ($P > 0.1$).

Widths of otolith increments formed when fish were fed 4% B.W./24 h and subjected to a 10-min bout of activity were not significantly different from widths of increments in fish which received two feedings equivalent to the 4% B.W./24 h ration level (t-test, $P > 0.05$). However, fish fed a ration of 8% B.W./24 h with two feedings produced increments whose average width was significantly greater than the latter two treatments (analysis of variance and the Student-Newman-Keuls test, $P < 0.01$). Mean increment widths in fish fed 4% B.W./24 h and exposed to a constant water-temperature regime were compared with increment widths in fish receiving the same ration plus

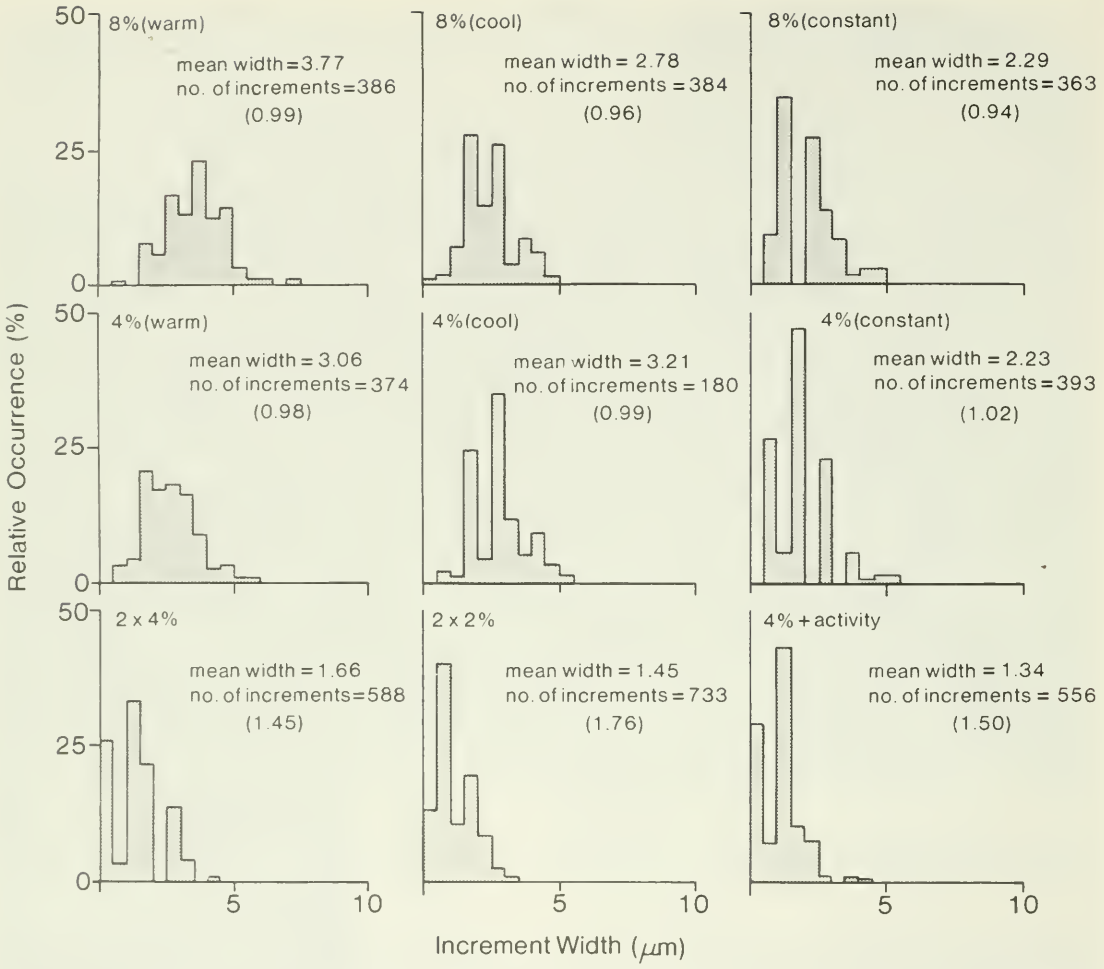

FIGURE 4.—Distribution of otolith increment widths under the experimental regimes. Treatments are identified by numbers in the top-left corners of histograms and correspond to treatments listed in Table 1. The average rate of increment formation every 24 h is shown in brackets.

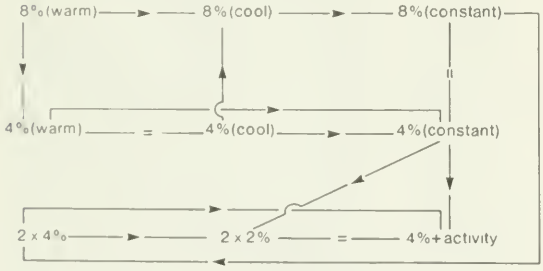

FIGURE 5.—Summary of Student-Newman-Keuls or t-test (α = 0.05) comparisons of mean increment widths in *Oncorhynchus tshawytscha* fry held under the various experimental regimes. Arrow heads pointing left or right signify "less than" and "greater than" respectively.

a 10-min period of enforced activity. The mean increment width associated with the latter treatment was significantly less (t-test, $P < 0.01$).

Production of the narrower growth increments associated with 2 feedings/24 h or 1 feeding and induced activity did not occur immediately upon commencement of the experimental regimes. A period of transition in otolith microstructure was evident. Figure 6 shows the decrease in increment widths with time in fish previously provided a ration of 8% B.W./24 h in one feeding and then offered the same total ration in 2 feedings/d. For comparison, data on increment widths in fish fed 8% B.W./24 h are provided (Fig. 6). The slope of the regression of increment width on date in the latter

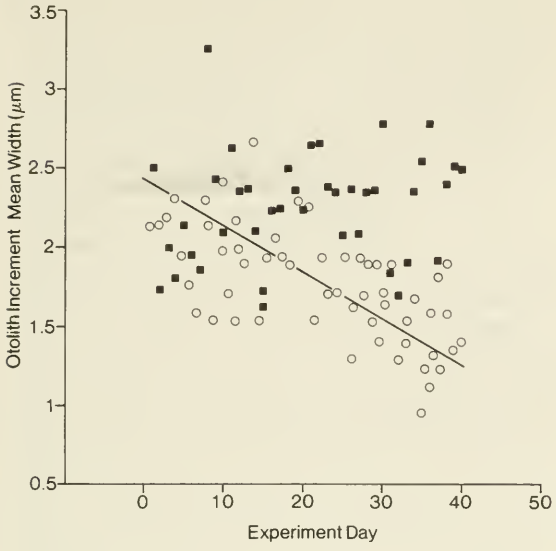

FIGURE 6.—Mean otolith increment widths (0) for *Oncorhynchus tshawytscha* fry from the 2 × 4% experimental feeding regime over days 1-40. Prior to day 1, fish were fed once every 24 h. Also shown are mean increment widths (■) of fish from the 8% (constant) feeding regime, where fish received one feeding only every 24 h.

treatment did not significantly differ from zero ($P > 0.10$), whereas the former did (t-test, $P < 0.01$).

Starved fry continued to produce one otolith increment every 24 h. However, the growth increments were faint when observed with a transmitted light microscope. That portion of otolith growth formed under starvation conditions was more transparent than the portion of otolith growth produced when fish were fed. Growth increment diel periodicity was also more pronounced during the portion of otolith growth corresponding to that period when fish were fed (Fig. 7).

To confirm that increment widths were proportional to fish growth, we plotted instantaneous growth in dry weight against average increment width for all treatments except the starved group (Fig. 8). The coefficient of determination (r^2) associated with those treatments in which fish formed 1 growth increment/24 h was 0.735 and the slope of the regression was significantly different from zero ($P < 0.01$). Note that points associated with treatments in which fish formed more than 1 increment/24 h lie considerably above the regression. The regression of these data differs signifi-

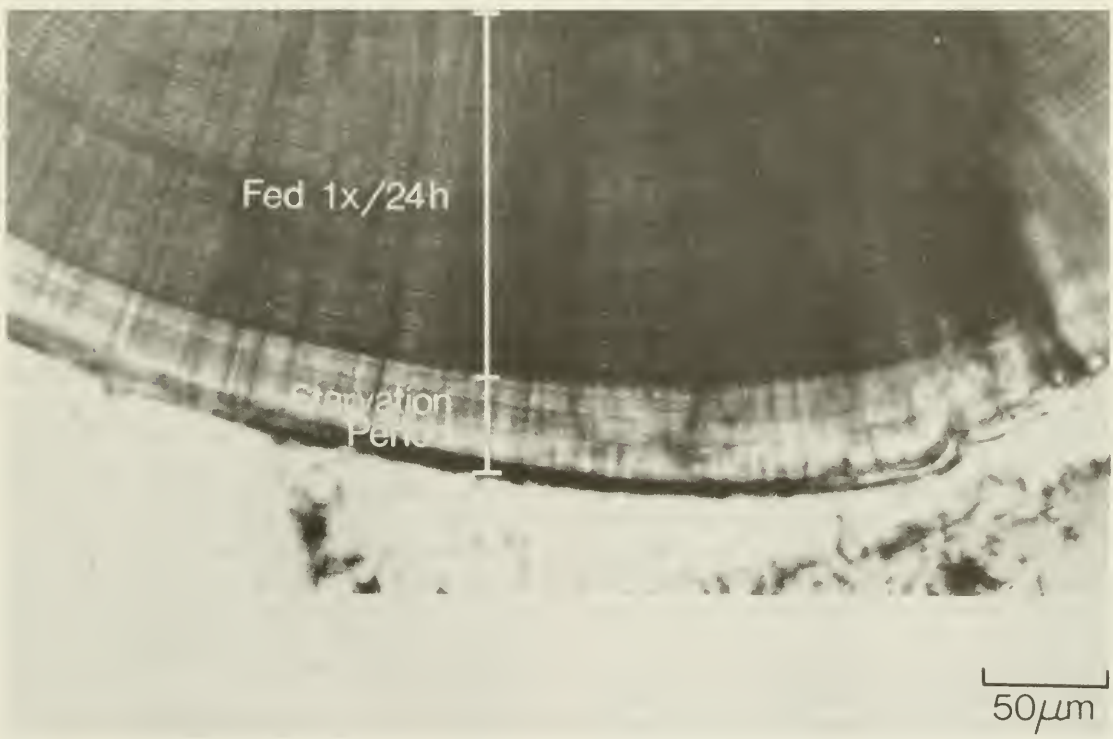

FIGURE 7.—Example of otolith microstructure from a starved *Oncorhynchus tshawytscha* salmon fry when viewed with transmitted light microscopy. The relatively transparent region near the otolith periphery corresponds to the starvation period.

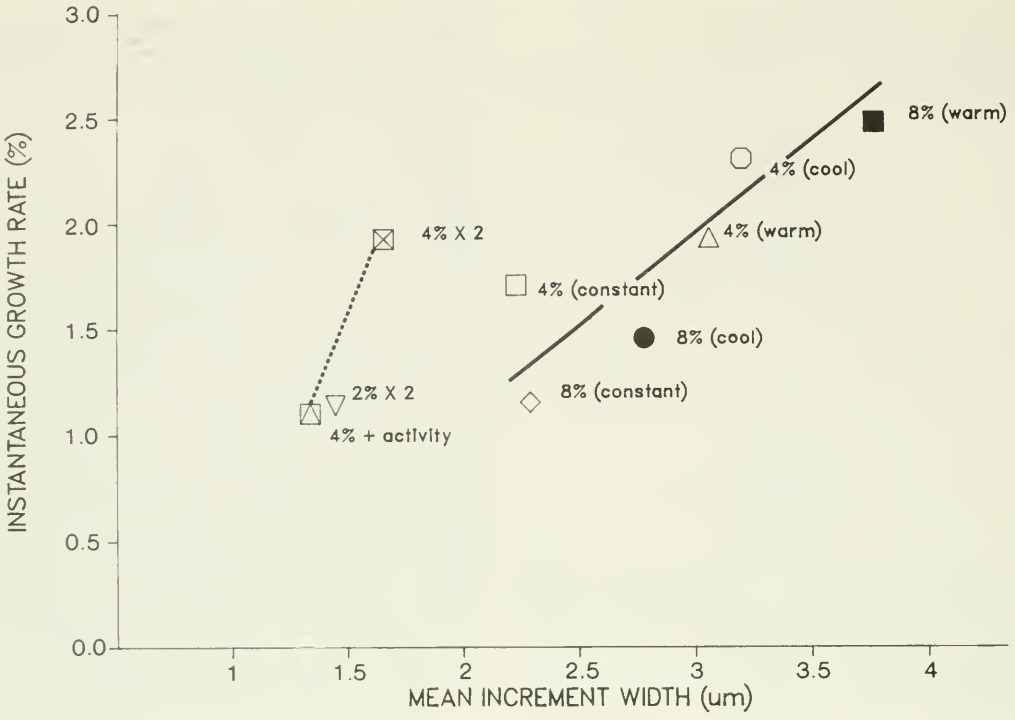

FIGURE 8.—Regressions of mean otolith increment width versus instantaneous growth rate (dry weight) for the various experimental regimes. Solid line represents groups where fish produced one increment every 24 h on average; dashed line represents treatments where fish produced significantly more than one increment every 24 h.

cantly in both slope and y-intercept (analysis of covariance and t-test, $P < 0.01$) from that of fish fed once per day.

Slopes of arithmetic mean linear regressions of fish dry weight on experiment day indicated that the average rate of growth of fish fed 8% B.W./24 h at the beginning of the warm portion of the diel temperature cycle was significantly greater than that of fish fed at the beginning of the cool period of the diel temperature regime or at the constant water temperature (6°C) (analysis of covariance and the Student-Newman-Keuls test, $P < 0.01$). Similar analyses among treatments in which fish were fed 4% B.W./24 h [4% (warm), 4% (cool), 4% (constant)] or among fish that received two feedings or one feeding coupled with an additional bout of activity ($2 \times 4\%$, $2 \times 2\%$, 4% + activity) indicated no significant differences in growth rate ($P > 0.05$).

To determine whether otolith growth-fish growth relationships were similar among treatments, we calculated otolith weight-fish dry weight regressions for data from all experimental regimes. Analysis of covariance indicated that the slopes of the predictive regressions among groups of fish fed 8% B.W./24 h and exposed to different temperature regimes did not significantly differ from each other ($P > 0.1$). Nor were there significant differences among treatments in which fish were fed twice/24 h or fed once/24 h and exposed to an enforced 10-min bout of activity. The slope of the regression representing the otolith weight-fish weight relationship for those fish receiving a ration of 4% B.W./24 h on the cool portion of the diel cycle was significantly greater than the slopes of regressions representing fish fed 4% B.W./24 h (warm or constant) (analysis of covariance and the Student-Newman-Keuls test, $P < 0.05$). However, as mentioned earlier, the treatment where fish received a ration of 4% B.W./24 h on the cool portion of the diel temperature cycle was affected by an interruption in water supply. Only five fish survived to day 40 and may not have been representative of fish held under those conditions.

DISCUSSION

Under most environmental conditions consid-

ered during this study and reported by Neilson and Geen (1982), one otolith growth increment was formed each day. This supports the hypothesis that an endogenous rhythm influences growth increment formation. Earlier, Neilson and Geen (1982) reported that multiple feedings within a 24-h period resulted in the formation of >1 increment/24 h. We suggested that this resulted from the interaction of an endogenous diel rhythm of increment production and some regularly recurring environmental event. Data presented here are consistent with that view, as increased feeding frequency, exposure to a warm/cool temperature cycle twice in 24 h and an enforced increase in fish activity were all associated with an increased rate of increment formation. The effects of at least some of these environmental events on otolith microstructure may be mediated through activity-induced modification of fish metabolism, which often follows a circadian rhythm (Matty 1978). If otolith growth increment production follows a circadian rhythm that is sometimes overlain by environmental events, it seems reasonable to assume that fish may produce one or more growth increments but not less than one every 24 h. In our studies, *O. tshawytscha* alevins and fry produced one or more growth increments every 24 h, a result consistent with most earlier studies. Even when fish were exposed to light and temperature stimuli with periods >24 h, Campana and Neilson (1982) reported that only one increment was formed every 24 h.

Diel water-temperature fluctuations were not required for otolith increment production in *O. tshawytscha*. However, cyclic changes in temperature with a 24-h periodicity apparently result in differences in the appearance of otolith growth increments (Fig. 2). The deeply etched portion of the increments is significantly wider in otoliths of fish taken from a diel water-temperature regime than those from fish held in water of constant temperature. Mugiya et al. (1981) concluded that the deeply etched portions of goldfish, *Carassius auratus*, otoliths have a relatively high concentration of protein relative to calcium carbonate. Degens et al. (1969) suggested that the deposition of the organic matrix is not readily modified by environmental events. If these results are applicable to salmonids, the greater contrast in otoliths of fish reared under a diel temperature regime may result from changes in the rate of calcium carbonate deposition. However, the presumed change in composition and structure of daily growth increments produced under various environmental conditions does not affect the increment width-fish growth relationship illustrated in Figure 8.

Interactions between ration level and time of feeding with respect to the 24-h temperature cycle affected mean increment width. Ration level as a single factor influencing increment width was not significant. However, the interaction between temperature and ration on increment width was not significant suggesting higher calcium carbonate deposition on the otolith when temperatures were elevated at time of feeding. In a two-way comparison with ration level and feeding frequency (water temperature was constant), increment width was affected by feeding frequency but not by ration level. This agrees with the results of Neilson and Geen (1982) who showed that the rate of increment production is affected by feeding frequency.

Mean increment width reflected fish growth under a variety of water-temperature and ration regimes (Fig. 8). However, different equations described increment width-growth relationships under conditions that produced 1 increment/d or >1 increment/d (Fig. 8). The extent to which increment width data can be used to predict instantaneous growth rates in natural populations remains to be examined.

Increment widths can provide an indicator of environmental changes and consequent alteration of growth rates. However, such changes, at least under laboratory conditions, did not occur rapidly (Fig. 6). These data suggest that at least 3 wk would be required before the change in increment width would be statistically detectable.

Our data indicate that otolith weight-fish weight regressions are similar under a range of experimental conditions suggesting that otolith growth in salmon fry is closely coupled to fish growth. Marshall and Parker (1982) also reported that differences in ration and water temperature did not significantly affect slopes of otolith size-fish size regressions among fed sockeye salmon, *O. nerka*, fry. Exceptions to the isometric growth relation between fish size and otolith size have only been observed in recently hatched salmonid alevins (Neilson unpubl. data) and in starved *O. tshawytscha* fry. Fry deprived of food for 19 d continued to form daily growth increments. Assuming fish dry weight did not increase over this period, then the slope of the otolith weight-fish weight regression would probably be greater than for fed fish. Marshall and Parker (1982) also reported continued otolith growth in *O. nerka* fry

over a 2-wk starvation period. Evidently continued otolith growth in starved fish resulted from the metabolism of stored energy reserves.

Estimates of food consumption indicated that fish held under diel cyclic temperatures and fed 8% B.W./24 h consumed significantly more food per gram of fish when the food was offered during the warm period (t-test, $P < 0.01$). No differences in food consumption were noted in fish receiving a 4% B.W./24 h ration on either the warm or cool portion of the diel water-temperature regime (t-test, $P > 0.05$). It is likely that fish were not satiated at this ration under either water-temperature regime. Under the high ration, fish were satiated even when the food was offered during the cool period of the water-temperature cycle. Additional consumption occurred only if food was offered during the warm portion of the diel temperature cycle. The additional food consumption was associated with increased growth rates. It is not clear whether the increased growth was simply a response to differences in food consumption or also reflected enhanced efficiency of food utilization in fish exposed to cyclic temperatures similar to that described by Brett (1979) and Biette and Geen (1980). Differences in growth rate of fish fed 4% B.W./24 h strongly suggest more efficient food utilization in fish exposed to a cyclic temperature regime. Food consumption did not differ although growth rates (and increment widths) are significantly greater.

Given that water temperature and food consumption are considered the most important features of fishes' environment affecting their growth (Paloheimo and Dickie 1966), it is not surprising that water-temperature regimes and ration levels influence otolith growth increment production. Our findings and those of English (1981) suggest that interpretation of prey abundance and feeding success from otolith microstructure data may be masked by relatively small changes in water temperature. Workers attempting to quantify fish growth with respect to ration size through examination of otolith microstructure should be aware of the effects of water temperature documented here and design studies accordingly.

ACKNOWLEDGMENTS

We thank Eldon Stone of the Canada Department of Fisheries and Oceans Capilano Hatchery for providing the fish used in this study. Tracey Crawford and Jeff Johansen assisted with otolith preparation. Ron Long, Department of Biological Sciences, Simon Fraser University, prepared the photographs. The critical review of an earlier draft of this manuscript by S. Campana and M. Healey is particularly appreciated. This work was supported by grants from Canada Department of Fisheries and Oceans and the Natural Sciences and Engineering Research Council to Glen H. Geen.

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U.S. DEPARTMENT OF COMMERCE

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Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115. Second class postage is paid at Seattle, Wash., and additional offices. POSTMASTER send address changes for subscriptions to Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

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The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 1 April 1985.

Fishery Bulletin

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USING OBJECTIVE CRITERIA AND MULTIPLE REGRESSION MODELS FOR AGE DETERMINATION IN FISHES

GEORGE W. BOEHLERT[1]

ABSTRACT

Analysis of the age structure of exploited fish populations is necessary for models upon which management decisions are made, but existing aging methodology for many species is hindered by subjective criteria used in age determination. A new technique is described in which age is estimated using multiple regression models based upon the measurable parameters otolith weight, otolith length, and otolith width in the splitnose rockfish, *Sebastes diploproa*, and the canary rockfish, *S. pinniger*. Models were calibrated using ages determined by interpretation of both whole otoliths and otolith sections which differ within these species, particularly at greater lengths. The models typically explained from 70 to 92% of the variability in age depending upon species, sex, and method of age analysis. In another sample used to verify the precision of the models, variability associated with model-estimated ages was generally less than that induced by variability in ages between different agencies. Based upon the pattern of otolith growth in length, width, and weight in these and other species, it is suggested that these methods would be applicable to a wide variety of fishes. Implementation of this type of age determination methodology could result in savings in time and cost for fisheries management agencies while decreasing variability among age estimates between different laboratories.

Virtually all methods of age determination in fishes involve a certain degree of subjectivity. Deciding whether a mark on an otolith or scale constitutes 1 year's growth is difficult; precision in fish aging improves only with experience. Even so, variability between experienced readers may be great. Sandeman (1969), for example, observed only 9% agreement between readers for a wide age range of otoliths of *Sebastes marinus* and *S. mentella*, and noted greater variability with increasing age of the fish. Kimura et al. (1979) suggested that bias between readers within a given agency is likely to be much less than among different agencies. In a situation such as exists on the Pacific coast, where several management agencies may routinely determine ages for the same species, interagency calibrations are necessary but are rarely achieved. Williams and Bedford (1974) suggested "...that otolith reading remains, for the present at least, as much an art as a science, and that proficiency cannot easily be achieved without examination of very large numbers of otoliths." Clearly, objective, repeatable age determination methodology which will minimize variability is desirable.

Traditional methodology for age determination in fishes generally involves some calcified structure; in *Sebastes*, Six and Horton (1977) tested 25 different structures. By far the most commonly used structures, however, are the otolith and scales. Scales are often best for short-lived, fast-growing species because annuli become indistinct near the margin in long-lived, slower growing species (Power 1978; Maraldo and MacCrimmon 1979). When this is the case, the otolith becomes the superior structure for age determination; even in the otolith, however, annuli may become indistinct on the margin as otoliths thicken and become opaque with age. For this reason several investigators have used broken or sectioned otoliths to determine age from internal banding patterns. While some studies using otolith sections have provided clear continuation of growth patterns obvious on whole otoliths from younger specimens, others have suggested maximum ages which are double or triple those estimated from whole otoliths. Power (1978), for example, suggested ages of >50 yr in *Salvelinus namaycush* and *Coregonus clupeaformis* and provided confirming evidence based upon population structure. In the redfish, *Sebastes marinus*, Sandeman (1961) suggested that specimens exceeding 50 yr of age were present in the population; ages up to 80 yr have since been estimated (Sandeman[2]). Similarly, Beamish

[1]Oregon State University, College of Oceanography, Marine Science Center, Newport, Oreg.; present address: Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[2]E. J. Sandeman, Biological Station, St. John's, Newfoundland, Canada, pers. commun. July 1978.

Manuscript accepted April 1984
FISHERY BULLETIN: VOL. 83, NO. 2, 1985.

(1979b) estimated ages approaching 90 yr in certain Pacific species of *Sebastes*, including *S. alutus*. In the genus *Sebastes*, these estimates of extended longevity have recently been confirmed by Bennett et al. (1982), who used geochronological methods to confirm age in *S. diploproa*. Understanding population structure for such long-lived species will require a large number of age estimates using otolith sections. Routine sectioning and interpretation of otoliths, however, is a time-consuming process, and age structure would need to be determined frequently for management of an active fishery. In this paper I suggest a possible alternative method for age determination.

Otolith growth begins with the initial "focus" and thereafter by incremental concretions of calcium carbonate in the form of aragonite. Otolith size increases with increasing size and age of the fish. Differential addition of crystalline material to the otolith, however, results in a species-specific shape (Bingel 1981). In flatfish and certain other species, Williams and Bedford (1974) observed continued linear growth of the otolith with growth of the fish only until maximum size was achieved; beyond this time, the otolith began to thicken. This has been observed in several other species (Blacker 1974a). Linear measurements of the otolith (i.e., length and width) are directly related to fish length and show little variability, but otolith thickness and weight are highly variable in larger fish (Templeman and Squire 1956; Beamish 1979a, b).

Templeman and Squire (1956) observed that length and width of otoliths from slow- and fast-growing populations of haddock did not differ at the same fish length, whereas otolith weight was consistently greater in the slower growing (and therefore older) populations at a given length. The same trend appears to exist in some members of the genus *Sebates* (G. W. Boehlert unpubl. data).

Beamish (1979a) observed an increase in thickness of the hake otolith with increasing otolith section age and a nearly linear relationship of otolith thickness and otolith weight. If otolith thickness, and therefore weight, is a function of fish age, then if fish length (or otolith length, since the two are related) is known, one should be able to estimate fish age. This was suggested by Brander (1974) with Irish Sea cod. The objective of this study is to determine the trends of otolith growth in terms of thickness, length, width, and weight, and to determine the potential of these criteria for estimation of age in splitnose rockfish, *S. diploproa*, and canary rockfish, *S. pinniger*.

MATERIALS AND METHODS

Otolith Collection

Otoliths of *S. pinniger* and *S. diploproa* were collected during the 1980 West Coast Survey conducted by the Northwest and Alaska Fisheries Center on the FV *Pat San Marie* and the FV *Mary Lou*. Gear and sampling strategy were similar to that described in Gunderson and Sample (1980). Otoliths were collected from fish captured in all hauls until desired numbers of specimens in specified length categories were obtained. Both otoliths from each specimen were removed, cleaned, and stored in individual, labeled vials containing 50% ethanol. Data taken with each specimen included vessel, haul (with latitude, longitude, and bottom depth), sex, and fork length (to the nearest 0.1 cm). After returning to the laboratory, otoliths were thoroughly cleaned and the preservative renewed.

Age Determination

General information on otolith morphology and whole otolith aging methodology in *Sebastes* is described in detail by Kimura et al. (1979). Age determined from whole otoliths followed the aging methodology of Boehlert (1980) for *S. diploproa* and that of Six and Horton (1977) for *S. pinniger*. Ages determined in this manner are referred to as whole otolith ages.

Otolith sections were prepared for selected specimens using the left otolith after the methodology of Nichy[3] with several modifications. Specimens were affixed to heavy-duty cardboard tags with double-faced tape and embedded in polyester casting resin in preparation for sectioning. Specimens were mounted in a chuck specifically designed to accommodate the cardboard tags and fed onto a pair of thin diamond blades separated by acetate spacers on a Buehler[4] low-speed Isomet saw. Dorsal-ventral sections through the focus and perpendicular to the sulcus, about 0.4 mm thick, were removed from the center of the otolith. Sections were removed from the tag and attached to labeled microscope slides with histological mounting medium. They were subsequently ground to eliminate surface artifacts,

[3]F. Nichy, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

first with 400-grit carborundum paper and then polished with 3 μm jeweler's rouge.

To compare internal otolith section annuli with surface annuli, 25 whole left otoliths from *S. pinniger* and 50 from *S. diploproa* were selected. Sample size was chosen to represent the range of ages estimated from whole otoliths. I determined the distance from focus to each annulus on the whole otolith along the dorsal-ventral axis from focus to dorsal edge of the otolith using an ocular micrometer on a dissecting microscope. These measurements were used to identify the first several annuli on corresponding sections. By following these identified annuli around to the internal dorsal surface it was determined that each small ring in the direction of counting (from focus to dorsal, interior surface) corresponded to a single year of growth (Fig. 1).

Sections were initially examined under a dissecting microscope at 30× magnification with either reflected light and a black background or transmitted light, depending upon the clarity of the annuli. Discerning and counting the narrow zones in otoliths from older fish was facilitated by the use of a compound microscope interfaced with a video camera and television screen. A more accurate estimate of age was made possible by the increased magnification and enhanced contrast of the compound microscope, coupled with the ease of viewing annuli on an enlarged screen.

Sections were aged by identifying the first translucent annulus (winter growth zone) and counting sequential growth zones from the center to the dorsal edge. Subsequent annuli were followed from the dorsal edge to the interior dorsal quadrant (after Beamish 1979b), and counted to the internal surface. In this paper, ages determined by different methods and sources will be discussed; none of these ages is known with certainty. For this reason, given ages will be defined as "standard ages" only for purposes of comparison.

Calibration Subsample

To establish models of age based upon otolith dimension and weight criteria, otoliths from the entire collection were subsampled. Every fourth otolith pair of *S. diploproa* and every third of *S. pinniger* were selected to provide roughly equal sample sizes representative of all sizes and collection (latitudinal) areas. These subsampled otoliths were used to develop the multiple regression models (see section on Data Analysis) and were treated as described below.

Whole otolith ages were determined by an experienced otolith reader to whom fish length remained unknown. This practice has been recommended by Williams and Bedford (1974), among others, to minimize bias in otolith reading. Otoliths were then dried to a constant weight at 58°C and placed in a dessicator for 8 h. Intact left otoliths were weighed to the nearest milligram. Otoliths were measured with dial calipers in the anteroposterior dimension (length) to the nearest 0.02 mm and in the maximum dorsoventral di-

FIGURE 1.—Dorsal-ventral section of the left otolith of a 305 mm FL female *Sebastes diploproa*. Whole otolith ages are generally determined from the focus (F) to the dorsal edge (A), but often extend to the posterior margin (not shown) which may include additional annuli extending to greater ages (A to B). Section ages are determined from the focus (F) to the internal dorsal surface (C). Note the additional growth zones on axis F-C which have been deposited after the latest visible zones on axis F-A. The otolith section age of this specimen is 40 yr.

mension (width) to the nearest 0.05 mm. When the left otolith was chipped or broken, the right one was substituted for measurements, since no systematic differences between left and right otolith measurements were apparent for either species. The left otolith was subsequently sectioned and age determined by the same otolith reader. Otolith thickness, which is too variable to measure on the whole otolith, was measured on the section from internal to external surface just dorsal to the sulcus (Fig. 1).

Confirmation Subsample

In order to test the precision of the model, subsamples of 50 otoliths by sex and species were drawn randomly from samples not used in the calibration subsample. These samples were handled in the following way: A second whole otolith age was determined by reader A to determine within-reader variability for *S. diploproa* and between-reader variability for *S. pinniger* (reader B had left this laboratory). The otoliths were sent to the Northwest and Alaska Fisheries Center (Seattle, Wash.) for an additional whole otolith age to determine between-agency variability. The otolith was dried, weighed, measured, and sectioned as described above; a single otolith section age for each specimen was determined by reader A for both species. Model-estimated ages were determined by use of the multiple regression models described below.

Data Analysis

Generally, data were recorded in a standard format and stored on the Oregon State University Cyber 70 computer. Data management and analysis were assisted by use of the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975).

From the calibration subsample of otoliths, predictive regression equations were developed to estimate age from otolith morphometrics. Multiple regression models were fitted in the following form:

$$\text{Age} = b_1X_1 + b_2X_2 + b_3X_3 + b_nX_n + c$$

where age (years) is determined by conventional methods, b_n's = regression coefficients, X_n's = independent variables, and c = constant. Models were developed for males and females separately within each species with both otolith section ages and whole otolith ages as dependent variables. Independent variables included otolith weight, otolith length, otolith width, the respective square and cubic terms of each, and the interaction variables (otolith weight/otolith length and otolith length/otolith width). With the exception of otolith weight, where both weight and the cube of weight were used as independent variables, square or cubic terms were not used if the raw values were entered. This decreased problems of multicollinearity. Models were fitted in a forward stepwise manner (Nie et al. 1975) with the inclusion level for independent variables set at $P = 0.10$.

The 1980 confirmation subsample was used to verify the models. Direct comparisons between ages determined for the same otoliths but different reading methods were accomplished by paired t-tests. Since age is not known with certainty for any otolith, the ages determined by reader A for *S. diploproa* and by reader B for *S. pinniger*, which were used to calibrate the models in the calibration subsample, were considered as "standard age". To conduct multiple comparisons of variability, deviations from standard age were defined as follows: "model-induced variation" is the difference between the standard age and the model-predicted age; "within-agency variation" is the difference between ages determined by reader A for *S. diploproa* and between readers A and B for *S. pinniger*; "between-agency variation" is the difference between the standard age and the age determined by the National Marine Fisheries Service (NMFS). A one-way analysis of variance (ANOVA) was used to compare these deviations. Multiple range testing was conducted using the least significance difference method with $\alpha = 0.05$. This analysis was conducted only for whole otoliths since only a single section age was determined on the 1980 confirmation subsample.

RESULTS

Sebastes diploproa

Locations of the collections of *S. diploproa* are shown in Figure 2; this species was taken from lat. 36°49′ to 48°47′N and over a depth range of 62 to 338 m. The distribution was similar to that noted in 1977 (Boehlert 1980). A total of 975 male and 1,145 female specimens were taken during the survey. The length frequencies show a mode near 23 cm for males and 24 cm for females with secondary modes at 26 and 27 cm, respectively. Corresponding age frequencies (based upon whole

otoliths) show a clear mode at 7 yr for both males and females, with whole otolith age ranges from 1 to 46 for males and 0 to 55 for females. Mean lengths-at-age for males and females are similar until age 8, after which females grow more rapidly (Boehlert 1980; Boehlert and Kappenman 1980).

Subsampling every fourth pair of otoliths from all collections of *S. diploproa* resulted in 290 female and 246 male specimens. The subsample was representative of the latitudinal distribution, age range, and length range of the whole collection. Capture, otolith, and age data from these samples are summarized in Table 1. Otolith section ages, as expected, were typically greater than whole otolith ages (Table 1); this was particularly true at greater lengths. Correlation matrices of pertinent otolith and age data (Table 2) show that otolith weight has the strongest linear association with otolith section age; both otolith weight and age are exponential functions of fish length. Plotting otolith length, fish length, and otolith weight against otolith section age demonstrates the pattern of otolith growth (Fig. 3). Past an age of about 25 yr, both otolith length and fork length reach approximate asymptotes, whereas otolith weight continues to increase. The wide fluctuations in otolith weight apparent at older ages correlate closely with changes in fork length (Fig. 3); for this reason, otolith weight alone is a relatively poor predictor of fish age at greater ages where fork length is highly variable. Addition of otolith

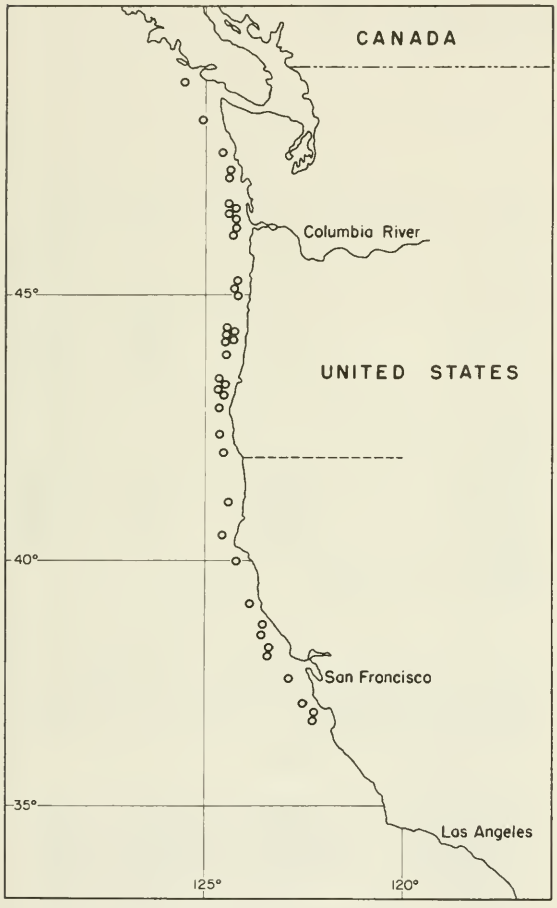

FIGURE 2.—Locations of 1980 West Coast Survey collections from which otoliths of *Sebastes diploproa* were taken.

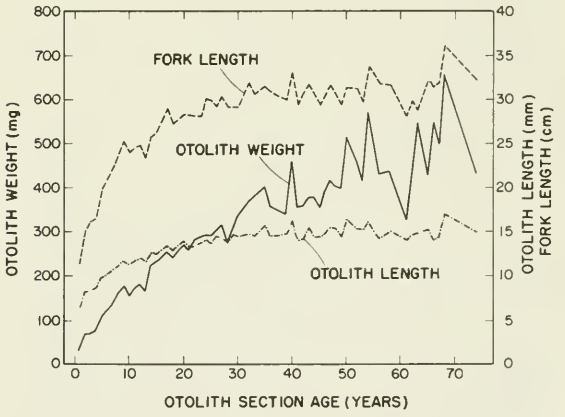

FIGURE 3.—Otolith characteristics of male *Sebastes diploproa* from the calibration subsample as related to fish length and age. $N = 246$. Note the covariation among the three curves, particularly at older ages.

TABLE 1.—Summary of biological and otolith data from the subsampled groups of *Sebastes diploproa* used in developing the age models.

Variable	Females ($N = 290$)				Males ($N = 246$)			
	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Depth of capture (fathoms)	34	185	137	29.36	53	185	136	28.45
Fork length (mm)	130	378	264	56.16	94	364	246	48.19
Otolith length (mm)	7.71	18.02	12.49	2.35	5.47	17.03	11.82	2.14
Otolith width (mm)	5.08	11.25	7.97	1.31	3.59	10.32	7.57	1.14
Otolith thickness (mm)	0.83	2.97	1.41	0.44	0.73	2.84	1.35	0.39
Otolith dry weight (mg)	59	724	244.6	150.4	25	659	208	117.4
Whole otolith age (yr)	1	56	15.2	11.97	1	40	13.5	9.78
Otolith section age (yr)	2	66	17.2	15.68	1	74	16.9	16.41

TABLE 2.—Correlation matrix for selected otolith morphometric, weight, and age data for the calibration subsample of *Sebastes diploproa*.

	Otolith weight	Otolith length	Otolith width	Otolith thickness	Whole otolith age	Otolith section age
Females (N = 290)						
Fork length	0.912	0.969	0.956	0.766	0.862	0.819
Otolith section age	0.947	0.859	0.788	0.938	0.917	
Whole otolith age	0.925	0.893	0.837	0.901		
Otolith thickness	0.930	0.843	0.778			
Otolith width	0.893	0.948				
Otolith length	0.940					
Males (N = 246)						
Fork length	0.895	0.971	0.959	0.815	0.835	0.769
Otolith section age	0.938	0.807	0.710	0.905	0.907	
Whole otolith age	0.923	0.885	0.778	0.846		
Otolith thickness	0.903	0.778	0.725			
Otolith width	0.857	0.778				
Otolith length	0.922					

length and the interaction variables compensate for these changes in the pattern of otolith weight in the multiple regression models of fish age.

The multiple regression models relating fish age with otolith data were fitted with both whole otolith age and otolith section age as dependent variables. Independent variables included in the whole otolith age models, their coefficients, and significance levels are presented in Table 3. All coefficients were highly significant and the models explain 88.1% of the variation in age for females and 92.0% for males, as measured by the coefficient of determination, R^2. Residuals from the models by age category show no trend up to age 35 for females and age 30 for males, after which there is a trend of increasing positive deviation with increasing age. The ages included in this part of the model, however, represented only 7.7% of female and 8.6% of male *S. diploproa* and are therefore not of great concern. These deviations are positive, however, suggesting that the model predictions may relate to otolith growth patterns which are more indicative of otolith section ages.

Variables included in the otolith section age models, their coefficients, standard errors, and significance levels are presented in Table 4. Again, all coefficients are highly significant, but the coefficients of determination are slightly less, explaining 86.1% of the variation in age for females and 85.0% for males. Mean residuals for the different age categories show no significant trend with age.

The model based upon whole otolith ages suffers from inaccuracies in the older ages, where otolith section ages are much greater than whole otolith ages. This is demonstrated in the trend of increasing residuals with increasing age. The model based upon otolith section age, however, is characterized by slightly lower multiple correlation coefficients (Table 4). This may be a result of inaccuracies in estimates of otolith section age of younger fish, where greater difficulty in age de-

TABLE 3.—Regression coefficients and associated statistics on the multiple regression models of whole otolith age for *Sebastes diploproa*.

Variable	Coefficient	SE	P
Females (N = 290)			
Otolith weight	0.1343	0.0091	<0.001
(Otolith weight)^3	-0.107×10^{-6}	0.14×10^{-7}	<0.001
Otolith width	−2.558	0.571	<0.001
Constant (a)	6.4303	3.004	0.033
SD = 4.15			
Multiple correlation, R = 0.939			
Males (N = 246)			
Otolith weight	0.2179	0.0145	<0.001
(Otolith weight)^3	-0.1945×10^{-6}	0.14×10^{-7}	<0.001
Otolith width	−3.4542	0.3942	<0.001
Otolith weight/length	−1.0997	0.2402	<0.001
Constant (a)	16.2572	2.2186	<0.001
SD = 2.797			
Multiple correlation, R = 0.959			

TABLE 4.—Regression coefficients and associated statistics on the multiple regression models of otolith section age for *Sebastes diploproa*.

Variable	Coefficient	SE	P
Females (N = 290)			
Otolith weight	0.2270	0.0137	<0.001
(Otolith width)^2	−0.3288	0.0377	<0.001
(Otolith weight)^3	-0.1134×10^{-6}	0.155×10^{-7}	<0.001
(Otolith length)^2	−0.1114	0.0205	<0.001
Constant (a)	5.0243	1.2982	<0.001
SD = 4.232			
Multiple correlation, R = 0.928			
Males (N = 246)			
Otolith weight	0.2496	0.0158	<0.001
Otolith width^3	−5.7233	0.6949	<0.001
(Otolith weight)^3	-0.1315×10^{-6}	0.266×10^{-7}	<0.001
(Otolith length)^2	−0.0882	0.0256	<0.001
Constant (a)	23.540	3.3823	<0.001
SD = 4.620			
Multiple correlation, R = 0.922			

termination exists with sections. For this reason, I also constructed a hybrid multiple regression model based upon a combination of otolith section and whole otolith ages. The decision on which age to use was arbitrary in the following way: If the difference (otolith section age minus whole otolith age) was ≤ 5 yr, whole otolith age was chosen; if the difference was >5 yr, otolith section age was chosen. The resulting models are described in Table 5. Independent variables similar to those in the other two models were chosen, and the multiple correlation coefficients were greater in each case.

To analyze the precision of the models, subsamples of 50 male and 50 female *S. diploproa* were taken from the remaining samples not used in the calibration subsample. Lengths and ages were representative of the respective ranges in the overall collection. Ranges of whole otolith age, NMFS age (that from the other agency), and otolith section age in these samples were 2-50, 3-49, and 2-75 for females and 3-34, 4-25, and 3-84 for males, respectively.

Whole otolith age was predicted based upon the appropriate whole otolith age models. Values of estimated age, whole otolith age, and NMFS age as a function of length are plotted in Figure 4. The deviation of NMFS age from whole otolith age increases with increasing length for both males and females. Deviations from the first whole otolith age are presented in Figure 5. Model-induced variability is the difference between estimated whole otolith age and whole otolith age; between-agency variability is whole otolith age minus NMFS age; within-agency variability is the difference of two successive age determinations by the same reader. Mean values of these sources of variation are presented in Table 6 for females and Table 7 for males. In both cases, the mean between-agency variability is greater than either model-induced or within-agency variability. One-way ANOVA demonstrates a significant difference among the three sources (Tables 6, 7). Multiple range testing (least significant difference, $\alpha = 0.05$), moreover, demonstrates that the means are significantly different for both females and males; the range tests suggest that within-agency and model-induced variability are equal and are both significantly less than the between-agency variability.

Only a single otolith section age was determined for specimens from the 1980 confirmation subsample. Ages were estimated from the multiple regression model of section age (Table 4) and compared with conventionally determined section age

TABLE 5.—Regression coefficients and associated statistics on the multiple regression models of age in *Sebastes diploproa*. The ages used for the calibration of these models are based upon either whole otoliths or otolith sections as described in the text.

Variable	Coefficient	SE	*P*
Females (N = 290)			
Otolith weight	0.2233	0.0135	<0.001
(Otolith width)^2	−0.2983	0.0403	<0.001
(Otolith weight)^3	-0.1244×10^{-6}	0.1685×10^{-7}	<0.001
Otolith length	−2.495	0.5084	<0.001
Constant (a)	17.7993	3.7339	<0.001
SD = 4.3967			
Multiple correlation, R = 0.962			
Males (N = 246)			
Otolith weight	0.2504	0.0157	<0.001
(Otolith width)^2	−0.3598	0.0549	<0.001
(Otolith weight)^3	-0.1272×10^{-6}	0.2800×10^{-7}	<0.001
Otolith length	−2.4123	0.6071	<0.001
Constant (a)	16.6069	3.9145	<0.001
SD = 4.7479			
Multiple correlation, R = 0.958			

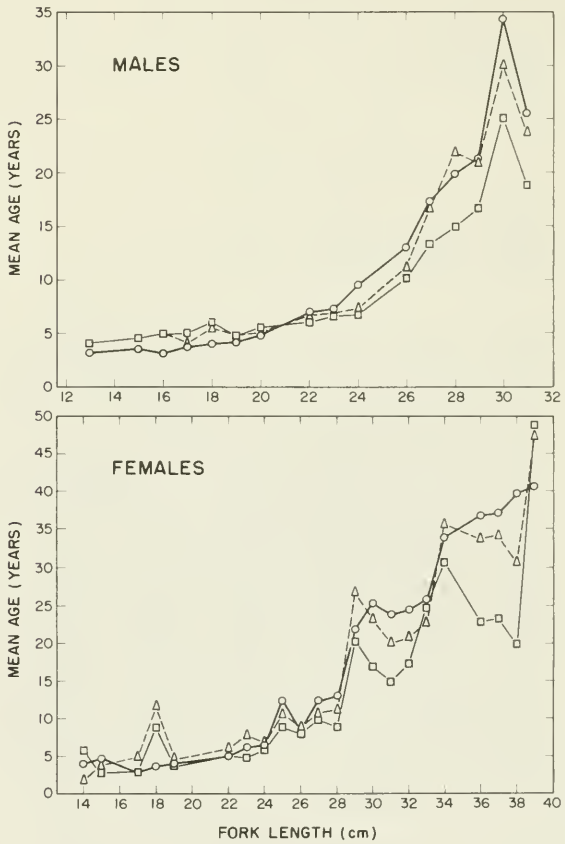

FIGURE 4.—Comparisons of mean whole otolith ages at length for the confirmation subsample of *Sebastes diploproa*. Triangles represent age from reader A, circles the age estimated by the model, and squares the age determined by another laboratory.

TABLE 6.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes diploproa* females. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, within reader variability.

Source		df	Sum of squares	Mean squares	F	P
Analysis of variance						
Between groups		2	707.77	353.89	23.14	0.001
Within groups		147	2,247.93	15.29		
Total		149	2,955.70			
Group	n	Mean	SD			
1	50	4.000	4.686			
2	50	−0.51	4.134			
3	50	−0.700	2.613			

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 3 = Group 2 < Group 1

TABLE 7.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes diploproa* males. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, within reader variability.

Source		df	Sum of squares	Mean squares	F	P
Analysis of variance						
Between groups		2	207.30	103.65	13.62	<0.001
Within groups		147	1,118.30	7.61		
Total		149	1,325.60			
Group	n	Mean	SD			
1	50	2.360	3.306			
2	50	0.108	2.294			
3	50	−0.320	2.575			

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 3 = Group 2 < Group 1

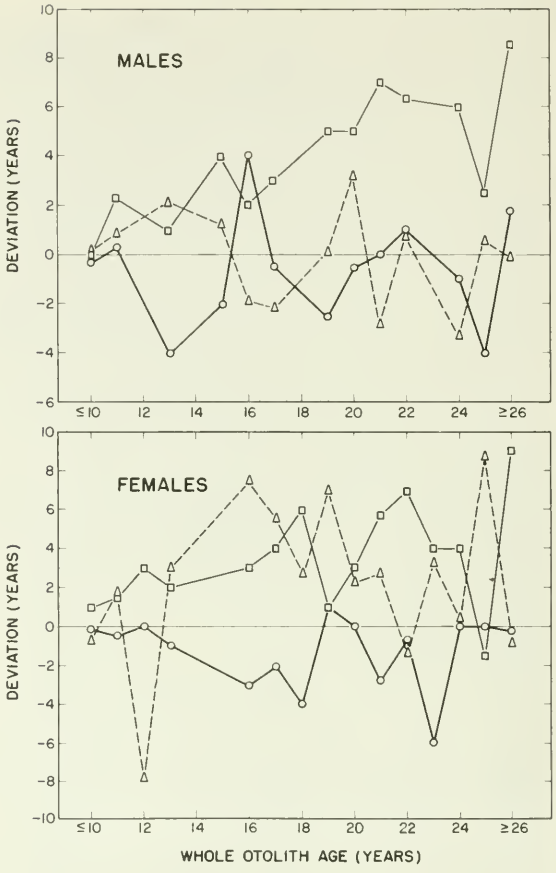

FIGURE 5.—Mean deviations of whole otolith ages from the confirmation subsample of *Sebastes diploproa*. Triangles represent model-induced variability, circles within-agency variability, and squares between-agency variability.

(Fig. 6). Ages were close to those predicted from the model with the notable exception of the maximum age for both males and females. In each instance, the maximum ages were greater than the maximum otolith section age in the calibration subsample; the estimated section age is therefore an extrapolation from the model. For the overall subsample, however, the estimated section ages were not significantly different from those determined by conventional methods (paired t-test, $\alpha = 0.05$). The observed and predicted ages comparing the confirmation subsample with the predicted ages from the hybrid model are not presented graphically, but the form of the curves for both males and females is virtually identical to that for the section age model (Fig. 6).

Sebastes pinniger

Sebastes pinniger were collected from lat. 43°11′ to 49°26′N at depths from 58 to 375 m (Fig. 7). Pairs of otoliths from a total of 519 male and 369 female specimens were taken from the survey. Length frequencies for *S. pinniger* show a mode at 50 cm for males and 52 cm for females. Age frequencies of the entire sample (based upon whole otoliths) demonstrate a mode for both males and females at 12 to 13 yr. Whole otolith ages from the collections ranged from 2 to 25 for males and 2 to 22 for females.

Subsampling every third pair of otoliths from the whole collection resulted in 171 male and 121 female specimens of *S. pinniger*. Again, this subsample was representative of the latitudinal distribution, age range, and length range of the whole sample. Capture, otolith, and age data from these specimens are summarized in Table 8. Otolith section ages in larger fish are generally greater than whole otolith ages, but not to the

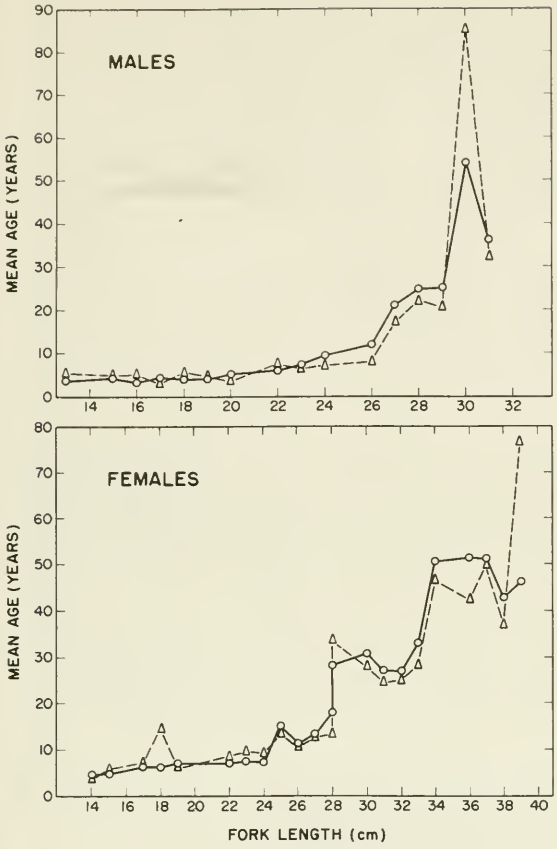

FIGURE 6.—Comparisons of mean otolith section ages at length from the confirmation subsample of *Sebastes diploproa*. Triangles represent otolith section age and circles the model estimated section age.

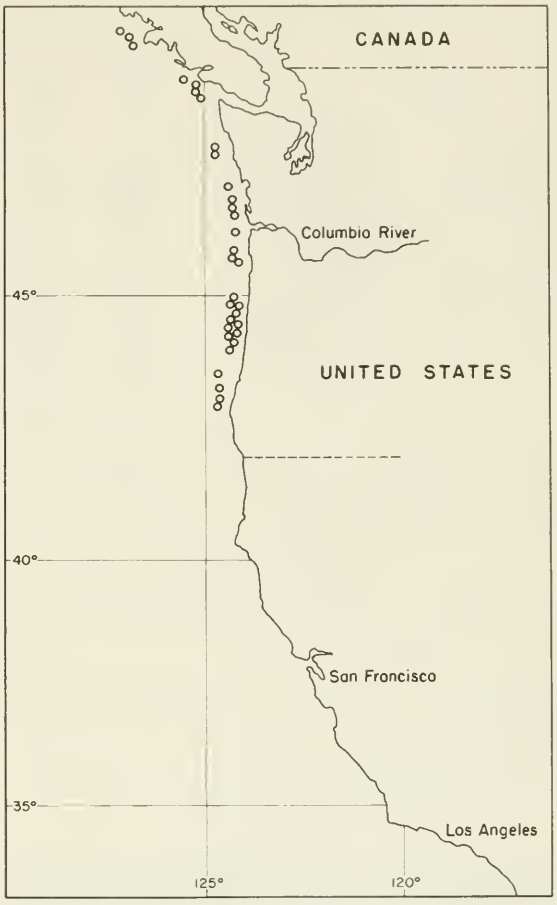

FIGURE 7.—Locations of 1980 West Coast Survey collections from which otoliths of *Sebastes pinniger* were taken for the current study. Samples from the FV *Pat San Marie* and the FV *Mary Lou* are included.

TABLE 8.—Summary of biological and otolith data from the subsampled groups of *Sebastes pinniger* used in developing the age models.

Variable	Females (N = 121)				Males (N = 171)			
	Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Depth of capture (fathoms)	32	100	69.8	12.66	37	103	73.3	14.39
Fork length (mm)	152	610	497.8	69.25	170	579	481.64	64.20
Otolith length (mm)	8.00	23.40	19.62	2.27	8.59	22.89	19.56	2.31
Otolith width (mm)	4.45	12.02	9.60	1.06	4.69	11.07	9.46	1.01
Otolith thickness (mm)	0.83	2.01	1.54	0.19	0.79	2.41	1.64	0.29
Otolith dry weight (mg)	53	821	486.7	135.5	58	867	517.0	160.69
Whole otolith age (yr)	2	19	12.4	3.16	2	25	13.2	3.79
Otolith section age (yr)	2	33	14.83	5.09	2	54	20.02	9.77

extent seen for *S. diploproa*. Otolith weight is again an exponential function of length, particularly for males. For females, however, this relationship was nearly linear. Of the ages determined in the calibration subsample, otolith weight has the strongest linear association with whole otolith age for females and whole otolith age and section age for males (Table 9).

The multiple regression models constructed to predict whole otolith age were based upon fewer variables than for *S. diploproa*, but included variables were highly significant (Table 10). The coeffi-

TABLE 9.—Correlation matrix for selected otolith morphometric, weight, and age data for the calibration subsample of *Sebastes pinniger*.

	Otolith weight	Otolith length	Otolith width	Otolith thickness	Whole otolith age	Otolith section age
Females (N = 121)						
Fork length	0.915	0.948	0.923	0.779	0.895	0.755
Otolith section age	0.825	0.735	0.757	0.718	0.795	
Whole otolith age	0.890	0.887	0.851	0.756		
Otolith thickness	0.826	0.765	0.756			
Otolith width	0.920	0.902				
Otolith length	0.917					
Males (N = 171)						
Fork length	0.844	0.940	0.909	0.754	0.847	0.682
Otolith section age	0.898	0.694	0.696	0.883	0.809	
Whole otolith age	0.892	0.837	0.815	0.830		
Otolith thickness	0.910	0.769	0.750			
Otolith width	0.869	0.901				
Otolith length	0.879					

TABLE 10.—Regression coefficients and associated statistics on the multiple regression models of whole otolith age for *Sebastes pinniger*.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith length)^3	0.00095	0.00011	<0.001
(Otolith width)^2	0.0448	0.0126	0.001
SD = 1.30			
Multiple correlation, R = 0.913			
Males (N = 171)			
Otolith weight	0.0280	0.00214	<0.001
(Otolith weight)^3	-0.845×10^{-8}	0.241×10^{-8}	0.001
SD = 1.665			
Multiple correlation, R = 0.900			

cient of determination (R^2) suggests that the models of whole otolith age explain 83.4% of the variation in age for females and 81.0% for males. For both males and females, the constant in the regression was not significantly different from zero and was not included in the models. The residuals from the models show no distinct trend with the exception of a slight increase at ages >17 yr for males; this included 11.1% of the sample.

The variables included in the otolith section age models, their coefficients, standard errors, and significance levels are presented in Table 11. As in the whole otolith age models, there are fewer variables included than for *S. diploproa*; for the male section age model, for example, there is only one variable and the constant included for prediction of age. All variables are highly significant and the coefficients of determination suggest that the otolith section models explain 70.2% of the variation in age for females and 84.6% for males. Mean residuals show a strong trend of increase at ages past 26 yr for male otolith section age models; this represented 23% of the sample.

A model incorporating both otolith section age and whole otolith age was developed using the same criteria for age as in *S. diploproa*. These models were based upon more independent variables but were not significantly better (as based upon the coefficient of determination) than the otolith section models (Table 12). Based upon the multiple correlation coefficients, the best models for *S. pinniger* would be the hybrid model for males and the whole otolith model for females.

For analyzing the precision of the models, sub-

TABLE 11.—Regression coefficients and associated statistics on the multiple regression models of otolith section age for *Sebastes pinniger*.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith weight)^2	0.272×10^{-4}	0.382×10^{-5}	<0.001
Otolith width	0.8368	0.4586	0.071
SD = 2.80			
Multiple correlation, R = 0.838			
Males (N = 171)			
(Otolith weight)^2	0.546×10^{-4}	0.179×10^{-5}	<0.001
Constant (a)	4.0297	0.6022	<0.001
SD = 3.85			
Multiple correlation, R = 0.920			

TABLE 12.—Regression coefficients and associated statistics on the multiple regression models of age in *Sebastes pinniger*. The ages used for the calibration of these models are based upon either whole otoliths or otolith sections as described in the text.

Variable	Coefficient	SE	P
Females (N = 121)			
(Otolith weight)^2	0.2621×10^{-4}	0.4518×10^{-5}	0.001
(Otolith width)^3	0.4038×10^{-2}	0.2186×10^{-2}	0.067
Constant (a)	3.2137	1.1296	0.005
SD = 2.8239			
Multiple correlation, R = 0.840			
Males (N = 171)			
(Otolith weight)^2	0.1306×10^{-3}	0.2359×10^{-4}	<0.001
(Otolith length)^3	-0.2044×10^{-2}	0.5456×10^{-3}	<0.001
(Otolith weight)^3	-0.6026×10^{-7}	0.2197×10^{-7}	0.007
Otolith length/width	9.7349	4.1381	0.020
Constant (a)	−12.8239	7.4064	0.085
SD = 3.9989			
Multiple correlation, R = 0.924			

samples of 50 male and 50 female *S. pinniger* were taken from the remaining 1980 samples not used in the calibration subsample. These subsamples were representative of the length and age ranges in the overall collection. Ranges of whole otolith age, NMFS age, and otolith section age in these subsamples were 4-26, 4-25, and 4-29 for females and 7-35, 7-32, and 8-45 for males, respectively.

Whole otolith age was estimated from the appropriate whole otolith age model for males and females. Values of model estimated age, whole otolith age, and NMFS age as a function of length are plotted in Figure 8. Female *S. pinniger* ages are similar for all three age determination methods. For males, model-estimated age is similar to the whole otolith age but both are less than the NMFS age (Fig. 8). Deviations from the whole otolith age by the otolith reader whose ages were used to calibrate the model are shown in Figure 9.

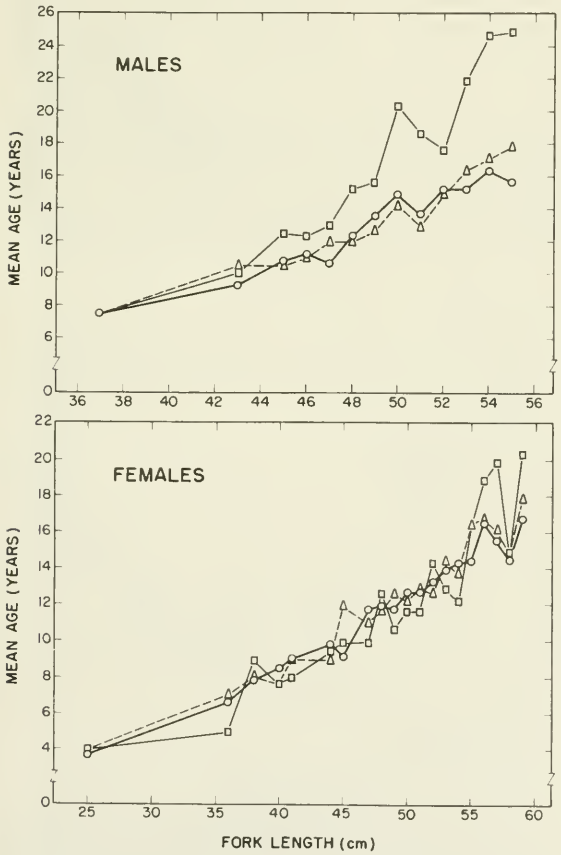

FIGURE 8.—Comparisons of mean whole otolith ages at length from the confirmation subsample of *Sebastes pinniger*. Triangles represent age from reader B, circles the age estimated by the model, squares the age determined by another laboratory.

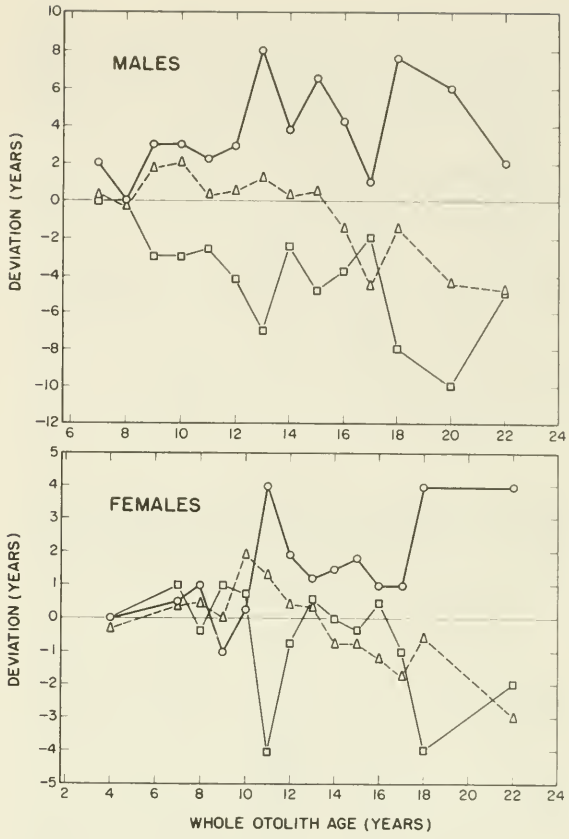

FIGURE 9.—Mean deviations of whole otolith ages from the confirmation subsample of *Sebastes pinniger*. Triangles represent model-induced variability, circles within-agency variability, and squares between-agency variability.

The explanation of these deviations is the same as for *S. diploproa* with the exception that the within-agency variability is a between-reader rather than a within-reader variability. One-way ANOVA within these deviations shows significant differences among the groups for both females (Table 13) and males (Table 14). Multiple range testing (least significant difference, $\alpha = 0.05$) demonstrates that for females, mean between-agency variability and model-induced variability are equal but are both less than within-agency variability (for *S. pinniger* this was based upon two different readers). For males, between-agency variability is less than model-induced variability which is less than within-agency variability. For the purposes of this comparison, however, the model-induced variability is significantly closer to zero than either of the other sources of variability (Table 14).

In the confirmation subsample, section ages estimated from the multiple regression model are

TABLE 13.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes pinniger* females. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, between reader variability.

Source		df	Sum of squares	Mean squares	F	P
Analysis of variance						
Between groups		2	88.69	44.34	8.67	<0.001
Within groups		147	751.84	5.11		
Total		149	840.53			
Group	*n*	Mean	SD			
1	50	−0.320	2.817			
2	50	−0.021	1.516			
3	50	1.44	2.260			

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 1 = Group 2 · Group 3

TABLE 14.—Results of one-way analysis of variance and multiple range tests comparing deviations of age from the standard age in *Sebastes pinniger* males. Group 1 = between-agency variability; group 2 = model-induced variability; group 3 = within-agency, between reader variability.

Source		df	Sum of squares	Mean squares	F	P
Analysis of variance						
Between groups		2	1,840.42	920.21	67.43	<0.001
Within groups		147	2,006.21	13.65		
Total		149	3,846.63			
Group	*n*	Mean	SD			
1	50	−4.280	4.427			
2	50	−0.111	2.107			
3	50	4.300	4.112			

Multiple range test (least significant difference, $\alpha = 0.05$)
Group 1 · Group 2 Group 3

compared with conventional section ages in Figure 10. The two ages are similar and as a whole are not significantly different for females but are significantly different for males (paired *t*-test, $\alpha = 0.05$). This is presumably a result of the consistently overestimated otolith section age for *S. pinniger* males. The ages estimated from the hybrid model (Fig. 11) are not significantly different from those determined by the appropriate conventional age (paired *t*-test, $\alpha = 0.05$).

DISCUSSION

The results of this research demonstrate the potential for using objective criteria and multivariate models to determine age in fast- and slow-growing members of the genus *Sebastes*. Past studies have used weight of the eye lens for estimates of age in fishes, amphibians, and certain mammals (Crivelli 1980; Malcolm and Brooks 1981). In fishes, however, this technique is only good for fast-growing species and provides poor estimates of age after several years when length at age becomes highly variable (Crivelli 1980); the same problems exist in estimating age from modal lengths. Growth of most body parts, including the eye lens, is allometric with length rather than age. Growth of the otolith, however, as described above, is a complex function of age as well as length. After a certain size is reached, the fish otolith does not increase in length or width, but continues to increase in thickness, and therefore weight, with age (Fig. 3). The increasing thickness is a function of addition of aragonite crystals only on the internal surface of the otolith (Fig. 1).

Similar patterns of otolith growth in length, width, thickness, and weight have been observed

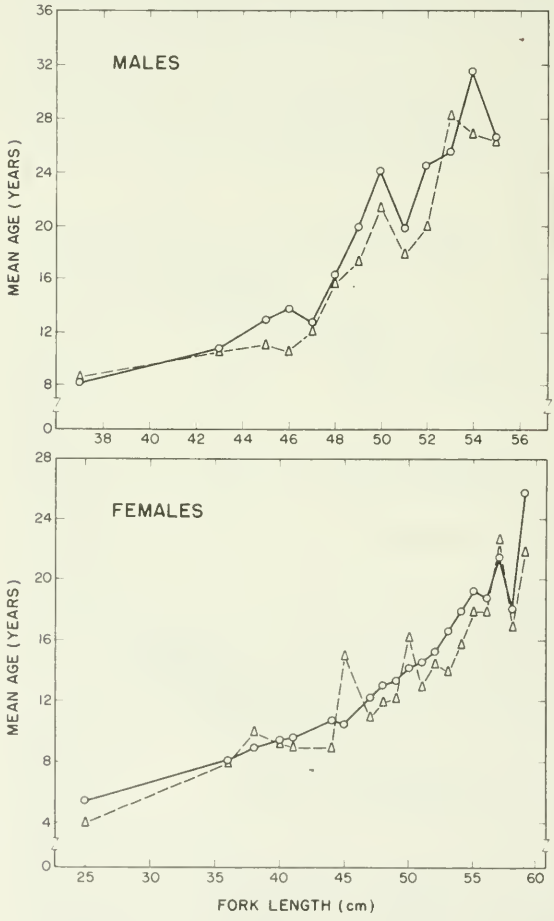

FIGURE 10.—Comparisons of mean otolith section ages at length from the confirmation subsample of *Sebastes pinniger*. Triangles represent otolith section age and circles the model estimated section age.

in other species of fish, but the information has not been applied to the estimation of age, with the exception of preliminary tests using discriminant techniques by Brander (1974). Templeman and Squire (1956), however, noted the importance of this information: "In many fishes, in which accurate age reading is doubtful, otolith weights, which are more factual, may offer a better separation of fish populations than growth rates which are dependent on the judgement of the scale- or otolith-reader." Weight and otolith measurements are valid criteria for age determination based upon the models (Tables 3-5, 10-12) and provide good estimates of age compared with other reading methods (Tables 6, 7, 13, 14; Figs. 4-6, 8-11). Based upon published patterns of otolith growth, these techniques should work for other species of *Sebastes* (Sandeman 1961; Beamish 1979b), Pacific hake (Beamish 1979a), haddock (Templeman and Squire 1956), plaice, sole, turbot, and horse mackerel (Blacker 1974a), and cod (Trout 1954; Blacker 1974a), among others. This technique may therefore be amenable to a wide variety of species of fishes.

Ages determined by scale or otolith readers are generally based on subjective decisions by the age reader, who reads annuli but must distinguish from "false checks", "metamorphic checks", and "spawning checks" (Trout 1961; Bailey et al. 1977).

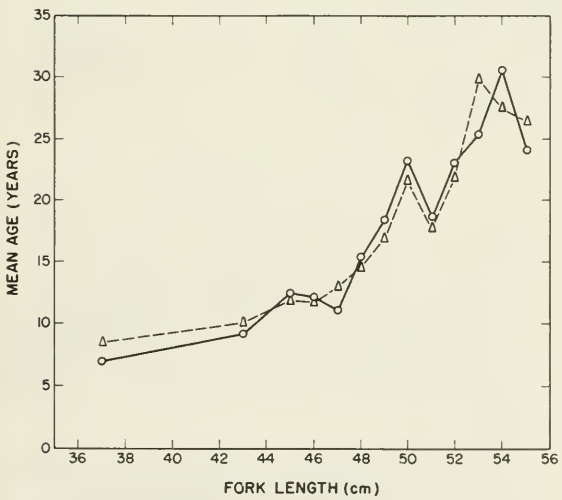

FIGURE 11.—Comparison of ages determined from otoliths and those predicted by the hybrid regression model for *Sebastes pinniger* males. Otolith ages were based upon whole otolith ages if the difference between section and whole otolith ages were ≤ 5; otherwise, otolith sections were used. Triangles represent whole otolith or section age and squares the model estimated age.

With experience comes reduced individual variability, but aging variability among different otolith readers and especially among different agencies is great; such variability can have important effects upon the estimates of growth parameters important for fisheries management (Sandeman 1961; Brander 1974; Hirschhorn 1974; Kimura et al. 1979). While otolith or scale exchanges are occasionally made between agencies for calibration purposes, this represents additional time spent for gaining greater consistency in ages (Westrheim and Harling 1973; Blacker 1974b), and difficulties may remain if disagreement in aging techniques cannot be resolved. Blacker (1974a) noted that "Recent progress in the use of otoliths for age determination has been limited mainly to the development of new techniques for preparing otoliths for reading and for photography so that aging methods can be readily compared." The techniques described in the present study represent a new approach to the systematic and repeated age determination in species for which continued age determination is necessary; once calibrated and implemented, the models would reduce between-reader and between-agency variability in age determination. Further research, however, should be conducted on variations in the models over seasons, regions, and different years to determine to what extent repeated calibration is necessary.

Ancillary benefits of the proposed methodology include its simplicity. Reliable, repeatable estimates of age require a great deal of experience on the part of an otolith or scale reader using conventional aging methodology (Blacker 1974a). It is often difficult to maintain a staff of trained otolith readers and retraining may require a large time commitment. The techniques described here require no special training, since the criteria (otolith length, otolith width, and otolith dry weight) are objective and can be measured with simple dial calipers and balance. Time expended for age determination by different methods is as follows: An experienced otolith reader averages about 17 ages/h on whole otoliths, but only 6 to 8 ages/h when otolith sections are used due to the additional preparation necessary. An untrained technician, however, can determine the measurements necessary for the model-based age estimates at a rate of about 40 otoliths/h on a long-term basis. Since the criteria for age are measurable, the techniques will be amenable to automation. Several attempts have been made in the past to automate or semiautomate age analysis using imaging

systems based upon differential light transmission (Fawell 1974; Mason 1974). These techniques have generally not been implemented, however, due to the subjective and variable nature of the criteria. Implementation of these techniques with automated systems could result in even further savings of time.

Since estimating the age distribution of exploited fish populations remains an important part of fishery biology, new and improved techniques of age determination are desirable. For shorter lived species, length-based methods are proving important (Pauly and David 1981). Age-length keys are also used quite extensively. Sample sizes necessary for accurate age-length keys, however, must be quite large, particularly for long-lived species such as *Sebastes*. In my relatively small calibration subsamples, for example, there are up to 15 age classes in a single 1 cm length interval (Table 15). Considering the maximum age of *S. diploproa* (Bennett et al. 1982), there could potentially be up to 50 age classes in a single length interval if a sufficient sample size were taken. For such species, age-length keys will be difficult to extrapolate meaningfully to the entire population without very large sample sizes, which must accordingly be aged. Similar, but more severe, problems will apply to techniques which attempt to extract growth parameters from length-frequency data for such long-lived species. The techniques developed by Pauly and David (1981) for faster growing species would be complemented by the current technique for slow-growing, difficult-to-age species. Otoliths could be collected by station, sex, and species without regard to size. From each otolith, after calibration of an age model, the available information could include both fish length and age. This approach to length data collection is not new and has been used by the International Pacific Halibut Commission for several years to estimate length (Southward 1962; Quinn et al. 1983). These techniques could therefore streamline not only the collection of otoliths at sea but also the analysis of age in the laboratory.

TABLE 15.—Number of age classes within single 1 cm length intervals from the calibration subsample. N = number of *Sebastes* specimens in the subsample.

Species	Sex	N	Whole otolith age	Otolith section age
S. diploproa	Female	290	14	14
	Male	246	12	14
S. pinniger	Female	121	6	11
	Male	171	9	15

The difficulty in age determination described above and the resulting variability between laboratories may have a negative impact upon accuracy of fishery models, particularly those using cohort or virtual population analysis (Brander 1974; Alverson and Carney 1975). The new methodology can provide significant time and cost savings over conventional methods and also decrease variability in age estimates. Implementation of these aging techniques, however, will require careful calibration with ages determined by a consensus of expert otolith readers from all management agencies with an interest in each species for which a model is developed.

ACKNOWLEDGMENTS

This research was supported by Cooperative Agreement No. 80-ABH-00049 from the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash. I thank Tom Dark, Mark Wilkins, and other participants in the 1980 West Coast Survey for assistance in specimen collection; particular thanks are extended to Captains Bernie and Tom Hansen of the FV *Pat San Marie* and MV *Mary Lou*, respectively, and their capable crews. Technical assistance and otolith reading were provided by Mary Yoklavich, Dena Gadomski, and Robert McClure. I thank Jack Lalanne for providing the NMFS age estimates. Finally, I thank W. H. Lenarz and D. R. Gunderson for critically reviewing the manuscript.

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RATES OF ATRESIA IN THE OVARY OF CAPTIVE AND WILD NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

J. ROE HUNTER AND BEVERLY J. MACEWICZ[1]

ABSTRACT

The process of ovarian atresia was described for northern anchovy using a laboratory group in which atresia was induced by starvation. Atretic characteristics of the ovary were described and illustrated, atretic ovarian states defined, and the rate that the ovary passed from one atretic stage to another was measured. The ovaries of starved females regressed rapidly; 3 days after the onset of starvation the ovaries of about half of the females contained yolked oocytes undergoing resorption of yolk (alpha stage of oocyte atresia) and by 23 days after the onset of starvation no yolk remained in the ovaries of any of the females. Gamma+delta stages of atretic follicles persisted in the ovary for over a month, but their decline in abundance indicated that eventually all signs of past reproductive activity would be lost in regressed ovaries.

In the natural population, rates of ovarian atresia increased seasonally from only a few percent of the females showing some atresia in peak spawning months to over 50% near the end of the season. Females with low levels of alpha stage atresia (<50% yolked oocytes affected) spawned about half as frequently as did those with no alpha stage atresia. Spawning was rare (1% of the females) or absent in females with high levels of alpha stage atresia (≥50% yolked oocytes affected). Late in the spawning season, it may be possible to forecast the end of spawning in the populations using the frequency of females in the populations with high levels of alpha stage oocyte atresia. Throughout the spawning season atretic rates were higher in small females (standard length ≤10 cm) than in larger ones indicating that 1-year-old females spawning for the first time have a much shorter spawning season than do older females.

Four approaches commonly used to determine the reproductive state of female fishes are 1) staging of ovaries using gross anatomical criteria such as the international Hjort scale (Bowers and Holliday 1961); 2) calculation of the gonosomatic index (GSI), i.e., gonad weight divided by female weight or the equivalent (de Vlaming et al. 1982); 3) estimating the mean diameter of the oocytes in the most advanced mode of oocytes (Hunter and Goldberg 1980; Hunter and Leong 1981); and 4) classifying ovaries histologically. Histological classification is superior to all other methods. Two of its great strengths are that the frequency of spawning of multiple spawning fish populations can be accurately estimated using the presence of postovulatory follicles (Hunter and Goldberg 1980) and that regressing ovaries can be distinguished from immature and from postovulatory ovaries. The histological criteria used to identify regressing ovaries is the presence of many oocytes and follicles undergoing resorption, a process known as atresia.

The interpretive power of histological analysis could be enhanced if the process of ovarian atresia were better documented. Specifically, ovarian atretic stages need to be defined, rates of atresia and duration of stages estimated, and the relation between ovarian atretic state and the probability of spawning determined. Such information would facilitate process oriented field studies on reproductive biology, and increase the accuracy of estimates of size at first maturity and size- or age-specific duration of the annual spawning season.

This study provides the laboratory and field calibration necessary for the assessment of the reproductive state of northern anchovy, *Engraulis mordax*, using the atretic condition of the ovary. We identify a range of ovarian atretic characteristics that define the atretic condition of the ovary, estimate rates of atresia, and estimate the duration that atretic characters persist in the ovaries of starving females in the laboratory. We use this information to classify ovaries of sea-caught females and estimate the probability of spawning for females with various levels of ovarian atresia.

We know of no similar work. A large descriptive

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted April 1984.
FISHERY BULLETIN: VOL. 83, NO. 2, 1985.

literature exists on follicular atresia in fishes (reviewed by Saidapur 1978) and stages of atretic oocytes and follicles have been defined (Bretschneider and Duyvene de Wit 1947; Lambert 1970a), but only the atretic rates in the guppy have been measured (Lambert 1970a). Considerable attention has been devoted to stages of atretic follicles (corpora atretica or "preovulatory corpora lutea") because of a presumed endocrine function (see reviews by Hoar 1965; Byskov 1978). The seasonal occurrence of atretic oocytes and follicles is often discussed as part of a general description of seasonal changes in the ovary of marine fish; see, for example, cycles described for the gobiid, *Gillichthys mirabilis* (de Vlaming 1972); plaice, *Pleuronectes platessa* (Barr 1963); *Paracentropristis cabrilla* (Zanuy 1977); and three species of *Epinephelus* (Bouain and Siau 1983). The proportion of females with atretic ovaries or the numbers of atretic oocytes within the ovary is given less often, but a few reports exist. For example, atresia ranged from 0 to 6% of the oocytes in female haddock, *Melanogrammus aeglefinus* (L.) (Robb 1982); corpora atretica increased to about 3% of the oocytes during the postspawning period of the dab, *Limanda limanda* (L.) (Htun-Han 1978); and atretic oocytes varied from 13% of yolked oocytes during the prespawning period to 100% during the postspawning period of the snapper, *Chrysophrys auratus* (F.) (Crossland 1977). Some attention has been given to the issue of whether or not atretic rates can account for differences in fecundity among females fed high and low rations. It appears that ration-related differences in fecundity are more closely tied to production rates of oocytes rather than atretic rates (Tyler and Dunn 1976; Wootton 1979). In summary, our literature review indicates that ovarian atresia has yet to be used for quantitative estimation of any reproductive processes in marine fish populations, although it has been used in general descriptions of the seasonality of reproduction for many years.

METHODS

Laboratory Experiment

Adult northern anchovy captured by commercial bait fishermen on 23 February 1982 were kept in a live car in San Diego Bay. Three days later about 1,000 fish averaging 104 mm SL (9.50 g) were taken to the laboratory and held in a 4.6 m diameter pool (1 m deep) at which time the first fish sample was taken. Over the first 34 d in captivity, samples of 18-24 females were taken at 3-4 d intervals with the final sample taken after 62 d in captivity. The temperature of the seawater ranged from 15.5° to 16.5°C.

The fish were not fed during the first 27 d in captivity because starvation was used to trigger the resorption of the ovary; thereafter they were fed daily. On the 27th day of starvation the ovaries had regressed from 4% of female body weight to 0.8% and feeding was resumed because we wished to learn how long the atretic characters would last once the fish began to feed.

In our calculations of atretic rates of laboratory females, we assumed that all the females at the time of capture had active ovaries without atresia, although no samples were taken until 3 d after the fish were captured. Only 3% of the 1,680 females taken in a survey conducted at the same time (28 January-8 March 1982) had atretic ovaries, and it was prominent in only 0.1% of the females (50% or more of yolked oocytes were affected). Ninety-six percent of the females in our first sample (taken 3 d after capture) had yolked eggs, and half of them had no atresia.

All females sampled during the course of the laboratory experiment were weighed and measured, and the ovary removed, weighed, and a section removed for histological analysis. Ovaries were fixed in 10% neutral buffered Formalin[2] and embedded in Paraplast. Histological sections were cut at 6 μm and stained with Harris hematoxylin followed by eosin counterstain.

Sea Data

The ovaries of northern anchovy taken in trawl surveys used for biomass estimation (Stauffer and Picquelle[3]) and various other collections from commercial seiners and midwater trawls were histologically examined. The number of females examined per catch (trawl, purse seine, or lampara net) has varied from 10 to 20. Some collections were quite small, especially those taken outside the main spawning season in the Southern California Bight; these small collections may consist of only two catches, whereas those taken during the main spawning months (February-March)

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Stauffer, G., and S. Picquelle. The 1980 and 1981 egg production estimates of anchovy spawning biomass. Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

were large, often consisting of 100 or more catches of 10-20 females each. In all collections ovaries were classed according to atretic characteristics as well as on the basis of the presence of postovulatory follicles (age 0 and age 1 d) and hydrated eggs according to the method described by Hunter and Goldberg (1980). All but two of the collections were from the Southern California Bight or northern Baja California, the region where the Central subpopulation of the northern anchovy is concentrated (Vrooman et al. 1981). Two collections were from the vicinity of Monterey and San Francisco Bays. Fish from these areas appear to have a different spawning season from those of fish to the south so they are listed separately in our seasonal tabulations. All collections were classified using histological criteria to determine the incidence of ovarian atretic states as a function of female size, season, and reproductive state.

Histological Characteristics

We describe below the histological characteristics of four oocyte classes and four stages of atresia in the northern anchovy. These stages and classes are subsequently used to define various ovarian atretic states in laboratory and sea-caught female anchovy.

Oocyte Classes

The northern anchovy is a multiple spawning fish (Hunter and Goldberg 1980) with asynchronous oocyte development (oocytes in many stages of development occurring simultaneously in reproductively active ovaries; Wallace and Selman 1981). During the spawning season oocyte development is a continuous process involving all stages with a new spawning batch maturing every week to 10 d (Hunter and Leong 1981). Oocyte development and maturation in teleosts, reviewed recently by Wallace and Selman (1981), has frequently been subdivided into many stages (Andrews 1931[4]; Yamamoto 1956; Lambert 1970b), but our work required a simpler histological classification system. We have combined the stages of past authors into four oocyte classes (unyolked oocytes, partially yolked oocytes, yolked oocytes, and hydrated oocytes), and we describe the histological characteristics of each class below.

1) Unyolked Oocytes—This class includes all oocytes without yolk that are about 0.04 mm or larger and range upward in size to about 0.35 mm (U, Fig. 1a, b). Oocytes <0.04 mm are excluded because they consist mostly of "oogonium nests", do not have a true follicle layer, and do not seem to undergo degeneration (o, Fig. 1b). The smaller oocytes within this class (0.04-0.15 mm) are spherical, have a large nucleus with a narrow homogenous very densely staining cytoplasm (Fig. 1b). A very thin single layer of elongated, spindlelike cells (the beginning of the granulosa layer) surrounds these small oocytes. The large oocytes in this class are oval, the cytoplasm stains faintly with hematoxylin and has a cloudy, mottled appearance (Fig. 1d). The oval nucleus of these oocytes contains several nucleoli and is surrounded by a granular perinuclear zone. In these larger oocytes a thin, definite, faintly eosinophilic staining, hyaline membrane (precursor of the zona radiata) appears between the oocyte and the growing follicle. The follicle consists of a narrow single inner layer of cuboidal granulosa cells and a single outer layer of flat elongated thecal cells with some blood capillaries. The larger oocytes also may have some small vesicles in the periphery of the cytoplasm. These vesicles are at times difficult to distinguish and they seem to disappear in yolked oocytes. No oil vacuoles exist as northern anchovy eggs do not contain oil droplets.

2) Partially Yolked Oocytes—Oocytes in this class are in the early stages of yolk deposition (vitellogenesis) and range in size from 0.3 to 0.5 mm (major axis) (P, Fig. 1d, g). The class includes oocytes in the initial stage of yolk deposition up to and including those in which yolk granules or spherules extend three-fourths of the distance from the periphery to the perinuclear zone. Yolk deposition starts at the periphery of the oocyte cytoplasm as small eosinophilic staining granules and then subsequently spreads internally until they nearly reach the finely granular perinuclear zone. Usually by this time the granules have become small spherules. The oval-shaped nucleus of oocytes in this class contains several nucleoli. Delicate striations appear on the hyaline membrane between the oocyte and follicle layer at the time yolk appears in the oocyte. As maturation proceeds, the follicle layer becomes wider due to an increase in the width and proliferation of granulosa cells. The thecal cells do not increase in size but remain elongated, flat cells with occasional blood capillaries and form a thin outer cov-

[4]Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. manuscr., 88 p. Stanford Univ., Stanford, CA 94305.

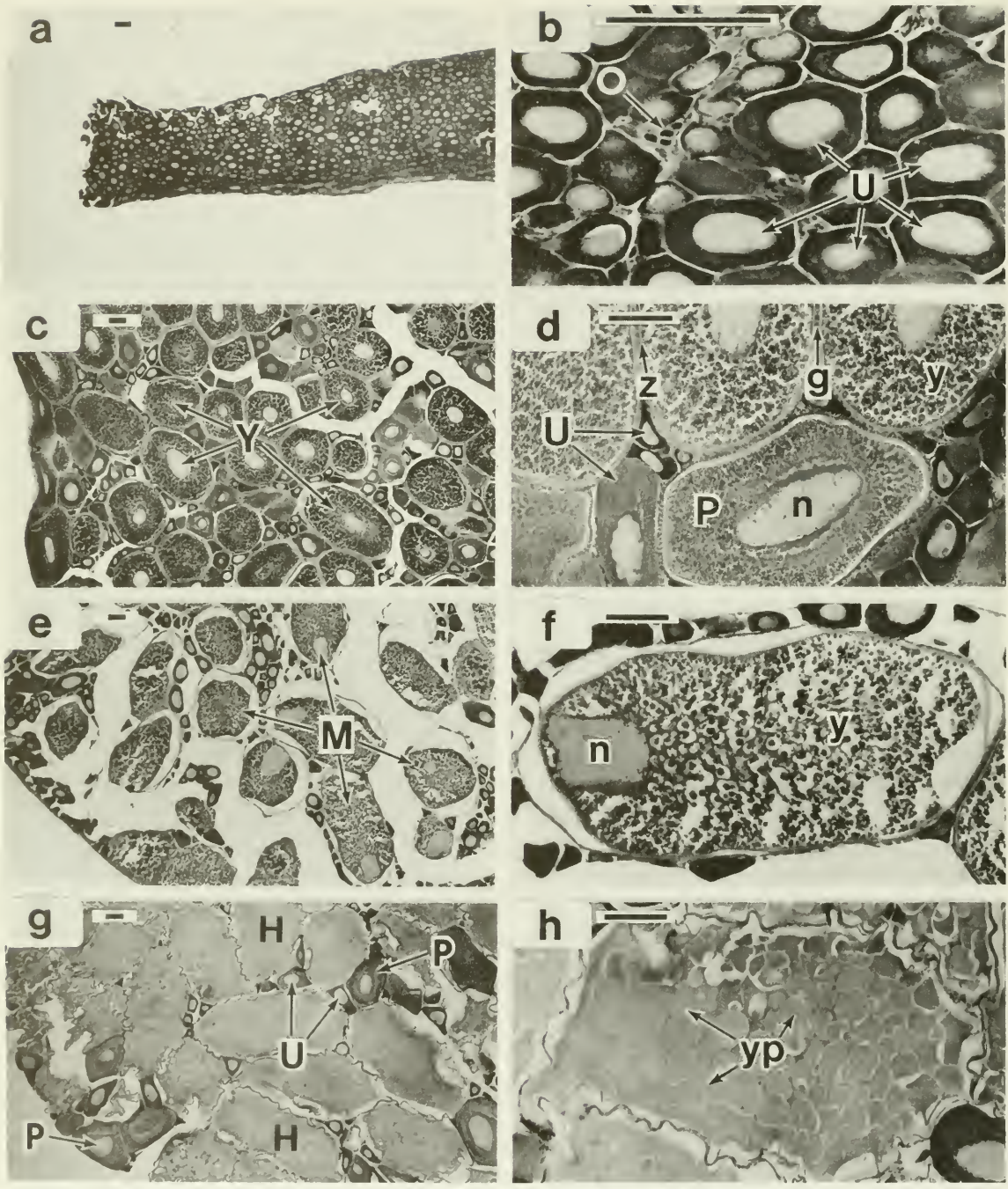

FIGURE 1.—Development of northern anchovy ovary at various magnifications (stain = H & E, bar = 0.1 mm). a) Immature ovary consisting of unyolked oocytes and no atresia. b) Enlargement of (a) showing small spherical unyolked oocytes (U) with a large central nucleus and "oogonium nests" (o). c) Normal mature ovary with many fully yolked oocytes (Y). d) All stages of oocytes: unyolked (U), partial yolked (P), and yolked (Y), are present in normal mature ovaries. (g = granulosa cell layer, z = zona radiata, n = nucleus, y = yolked globules.) e) Prespawning ovary showing migration of nucleus to the animal pole. f) Enlargement of a migratory nucleus oocyte (M). (n = nucleus, y = yolk globules.) g) Imminent (< 12 h) spawning ovary with hydrated oocytes (H) still within the follicle layer. (U = unyolked, P = partial yolked.) h) Enlargement of a hydrated oocyte. Note that the yolk globules have fused into yolk plates (yp) and there is no prominent nucleus due to disintegration of the nuclear membrane.

ering to the follicle. The thecal cells do not change until hydration when they become even flatter and have a stringy appearance.

3) Yolked Oocytes—Oocytes in this class range from 0.45 to 0.80 mm (major axis), and all contain yolk spherules or globules throughout the region between the periphery of the oocyte and the perinuclear zone (Y, Fig. 1c, d). As vitellogenesis continues, the yolk varies from spherules in the smaller oocytes to large globules in the larger ones. Just prior to spawning (<24 h) the globules fuse to form yolk plates (Fig. 1h). Such oocytes are excluded from this oocyte class, this characteristic being diagnostic of the last class (hydrated oocytes). The nucleus of oocytes in the yolked oocyte class is oval with numerous nucleoli. The granulosa cells have a wide rectangular shape in cross section and a large oval nucleus; their walls are clearly evident in sagittal section where they form polyhedrons. The zona radiata is a wide, striated, eosinophilic band until hydration when it stretches thin and the striations disappear.

4) Hydrated Oocytes—These oocytes range in size from 0.75 to 1.2 mm (major axis) (H, Fig. 1g, h). Hydration (rapid uptake of fluid by the follicle, Fulton 1898) begins when the nucleus has migrated to the animal pole (M, Fig. 1e, f) and yolk globules first fuse to form yolk plates, and it ends when the hydrated oocyte is ovulated. The nucleus of hydrated oocytes is not visible except in the earliest phase because after the nucleus migrates, the nuclear membrane disintegrates dispersing its contents into the cytoplasm. During hydration all yolk globules fuse into plates and the oocyte expands greatly, stretching the granulosa and thecal cell layers. At this time, the granulosa cells in cross section appear as long, thin rectangles, the thecal cells are extremely flat and have a stringlike appearance, and the zona radiata is very thin and lacks striations. Hydrated oocytes are the most ephemeral of all oocyte classes since this stage lasts for less than a day, whereas the other stages are always present in reproductively active anchovy ovaries. Migratory nuclei may be seen as early as 24 h before ovulation, but hydrated oocytes in which all globulues are fused to form yolk plates do not occur earlier than 12 h before spawning. We have never observed atresia in hydrated oocytes; apparently, in northern anchovy, nearly all hydrated oocytes are ovulated.

Atretic Stages

The nomenclature and general characteristics used for the four atretic stages given below follow those of Bretschneider and Duyvene de Wit (1947) and Lambert (1970a). In the initial stage of the atretic process (alpha (α)), the entire oocyte is resorbed including the yolk, if present, by the hypertrophying granulosa cells of the follicle. In the next stage (beta (β)), the major degeneration and resorption of the follicle (granulosa and thecal cells) occurs. In the third (gamma (γ)) and fourth (delta (δ)) atretic stages, regression of the theca and granulosa cells continues, greatly reducing the size of the follicle, and a yellow-brown pigment appears. The histological characteristics used to identify these stages are outlined below.

1) Alpha (α) Stage Atresia—In the alpha stage of atresia the oocyte is resorbing leaving only the follicular layers. The early phase of alpha stage atresia is characterized by the disintegration of the nucleus, evident by an irregular shape, and a granular, dark basophilic staining, and the disintegration of some of the yolk globules, indicated by less refractive globules, fused globules, or globules expanded and of less regular shape (Fig. 2a, b, c). The zona radiata slowly dissolves as indicated by the loss of striations and uneven diameter (Fig. 2b). In subsequent phases of alpha atresia, granulosa cells enlarge and, upon rupture of the zona radiata, invade the degenerating oocyte (Fig. 2d). Yolk adjacent to the invading granulosa cells liquifies (loses all structural integrity and appears as a homogeneous eosinophilic area) and becomes phagocytized by the granulosa cells as indicated by the presence of yolk in the vacuoles of these cells. The basophilic staining cytoplasm is also resorbed by the granulosa cells. In the alpha stage of atresia, blood capillaries and vessels are numerous in the thecal connective layer which does not proliferate or invade the oocyte but remains as a thin layer covering the granulosa cells. The alpha stage ends when resorption of the oocyte is complete (all cytoplasm and yolk are gone). The resulting structure (beta stage) is usually much smaller than the original oocyte. The subsequent atretic stages (beta-delta) are steps in the resorption of the remaining follicle and the structure at this point is called an atretic follicle, the term atretic oocyte being reserved for only the alpha stage of atresia.

In unyolked oocytes the alpha stage process is similar but without yolk (Fig. 2e, f). The nucleus

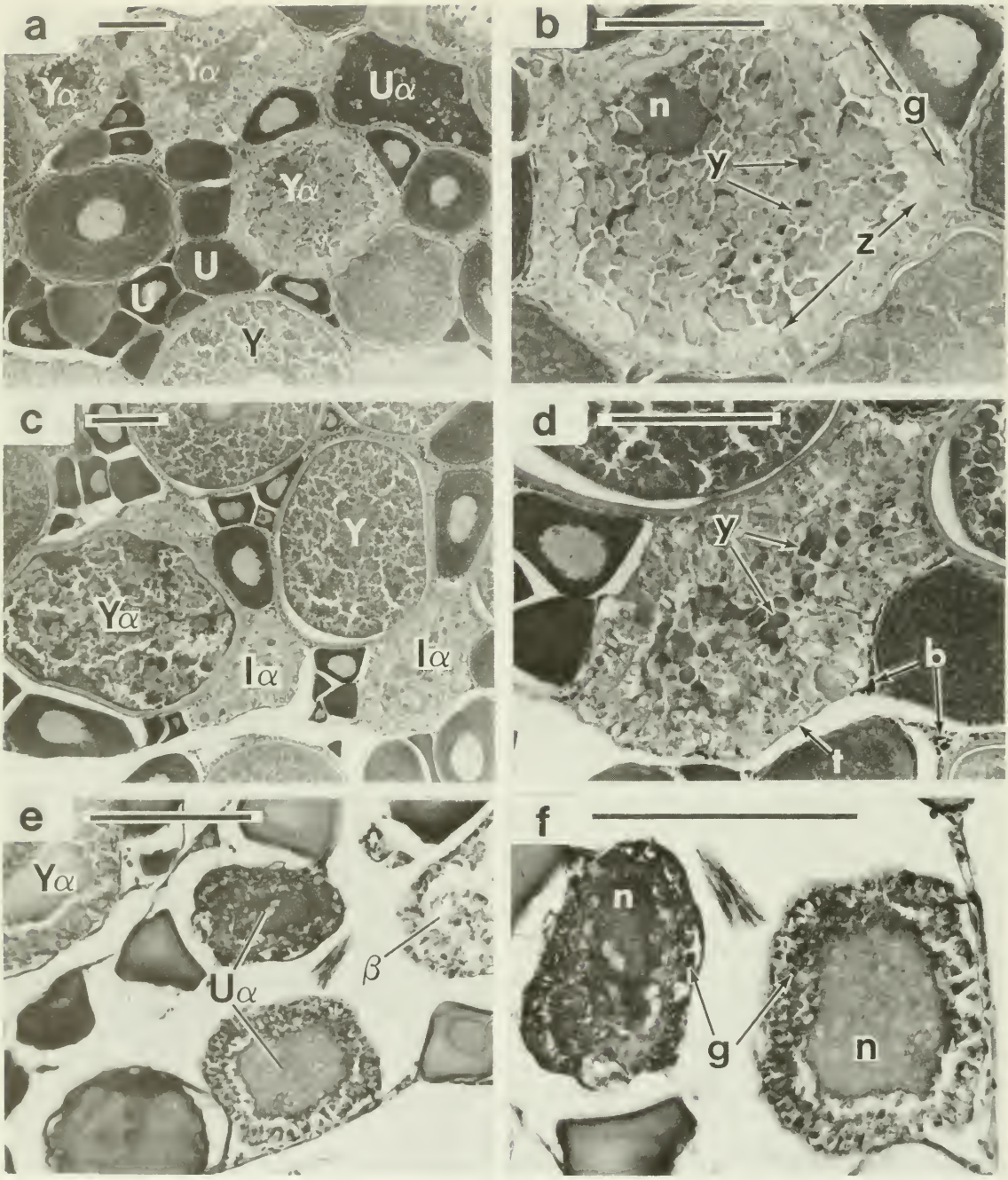

FIGURE 2.—Alpha (α) stage atresia in yolked (Y) and unyolked (U) oocytes (bar = 0.1 mm). a) and b) Yolked oocyte undergoing alpha atresia ($Y\alpha$). Notice dark irregular nucleus (n), uneven dissolving zona radiata (z), and hypertrophic granulosa cells (g); ($U\alpha$ = alpha atresia of a large unyolked oocyte). c) and d) Only remnants of yolk (y) remain among the invasive phagocytizing granulosa cells in this late phase of alpha atresia ($I\alpha$). Note also the thecal layer (t) and the closely associated red blood cells (b). e) and f) Unyolked oocytes in the alpha stage of atresia ($U\alpha$), note enlargement of granulosa (g) and disintegration of nucleus (n). ($Y\alpha$ = alpha yolked atretic oocyte, β = beta atresia.)

disintegrates, the thin prezona radiata (if present) dissolves and the granulosa cells enlarge, and, with only a slight proliferation, phagocytize the unyolked oocyte. When resorption is complete, all that remains is the follicle.

2) Beta (β) Stage Atresia—Initially the beta stage atretic follicle is a compact structure composed of numerous disorganized granulosa cells surrounded by a thin thecal and blood vessel layer. The nucleus of some of the granulosa cells is pycnotic and many of the cells contain a large intracellular vacuole that may be empty or contain amorphous particles. Occasionally one or more large intercellular cavities may exist among the granulosa cells (Fig. 3b, d). Preovulatory beta stage atretic follicles containing such cavities may easily be confused with postovulatory follicles (older than 48 h) and, as a consequence, we do not age postovulatory follicles older than 48 h (Hunter and Goldberg 1980). In addition, small (older) beta stage atretic follicles from yolked oocytes (Fig. 3c, d) are indistinguishable from beta stage atretic follicles from unyolked oocytes. Thus, we do not identify the original oocyte type undergoing atresia in beta or subsequent atretic stages; such distinctions are made only for alpha stage atretic oocytes.

Three different patterns of atresia may occur at the conclusion of the beta stage: 1) The follicle may follow the classic pattern outlined by Bretschneider and Duyvene de Wit (1947) and pass through subsequent gamma and delta stages (both characterized by increased pigmentation, see below); 2) the follicle may be completely resorbed during the beta stage leaving no histological characteristics that can be identified; and 3) the follicle may pass directly from a beta stage structure to a delta stage structure without passing through the intervening gamma stage. In northern anchovy, either the duration of the gamma stage is very short or few follicles pass through the gamma stage into the delta stage, because in regressing ovaries the incidence of gamma stages is very low compared with those of either beta or delta stages.

3) Gamma (γ) Stage Atresia—The gamma stage atretic follicle is usually much smaller than the typical beta stage follicle (Fig. 3e). The granulosa cells contain flocculent material of light-yellow hue and have nuclei of very irregular shape. The granulosa cells are surrounded by many fewer thecal cells and blood vessels than occur in the beta stage atretic follicles. Occasionally we see an atretic follicle of quite different appearance in anchovy ovaries which we classify as a gamma stage atretic follicle; they are included in the gamma stage because they also contain flocculent material of light-yellow hue. In this case, the flocculent yellow material is extracellular rather than intracellular, and the material is encapsulated by a layer of granulosa and thecal cells. It is possible that the extracellular flocculent material is produced by the disintegration of granulosa cells.

4) Delta (δ) Stage Atresia—The diagnostic characteristic of this stage is the presence of a dark yellow-brown, finely granular pigment in the granulosa cells (Fig. 3f). The delta stage atretic follicles are normally very small structures typically composed usually of 2-20 granulosa cells in the ovarian connective tissue stroma. Thecal cells and blood vessels no longer encompass the granulosa cells.

In our laboratory work 3-4 levels of abundance were recorded for each of three atretic classes seen in anchovy ovaries (alpha, beta, and gamma+ delta stages). The gamma and delta stages were combined since gamma stages were rare. In addition, the alpha stage atretic class was further subdivided into three groups depending on the type of oocyte undergoing atresia (unyolked, partially yolked, and yolked oocytes). In the discussion that follows we have combined some of the abundance levels and have considered only what we believe to be the most diagnostic atretic characteristics, although all atretic characteristics as originally tabulated are given in Tables 1 and 2. The system of atretic classifications was further simplified in our presentation of the analysis of sea-caught specimens, but that will be discussed subsequently.

RESULTS

Rates of Atresia in the Laboratory

The speed at which yolked oocytes were resorbed was striking. In the first sample (elapsed time from onset of starvation = 3 d) the ovaries of 11 of the 24 females (46%) had yolked oocytes in the alpha stage of atresia (Table 1). By the 13th day, half of the females no longer had yolked oocytes, and in the rest of the females 50% or more of their yolked oocytes were in the alpha stage of oocyte

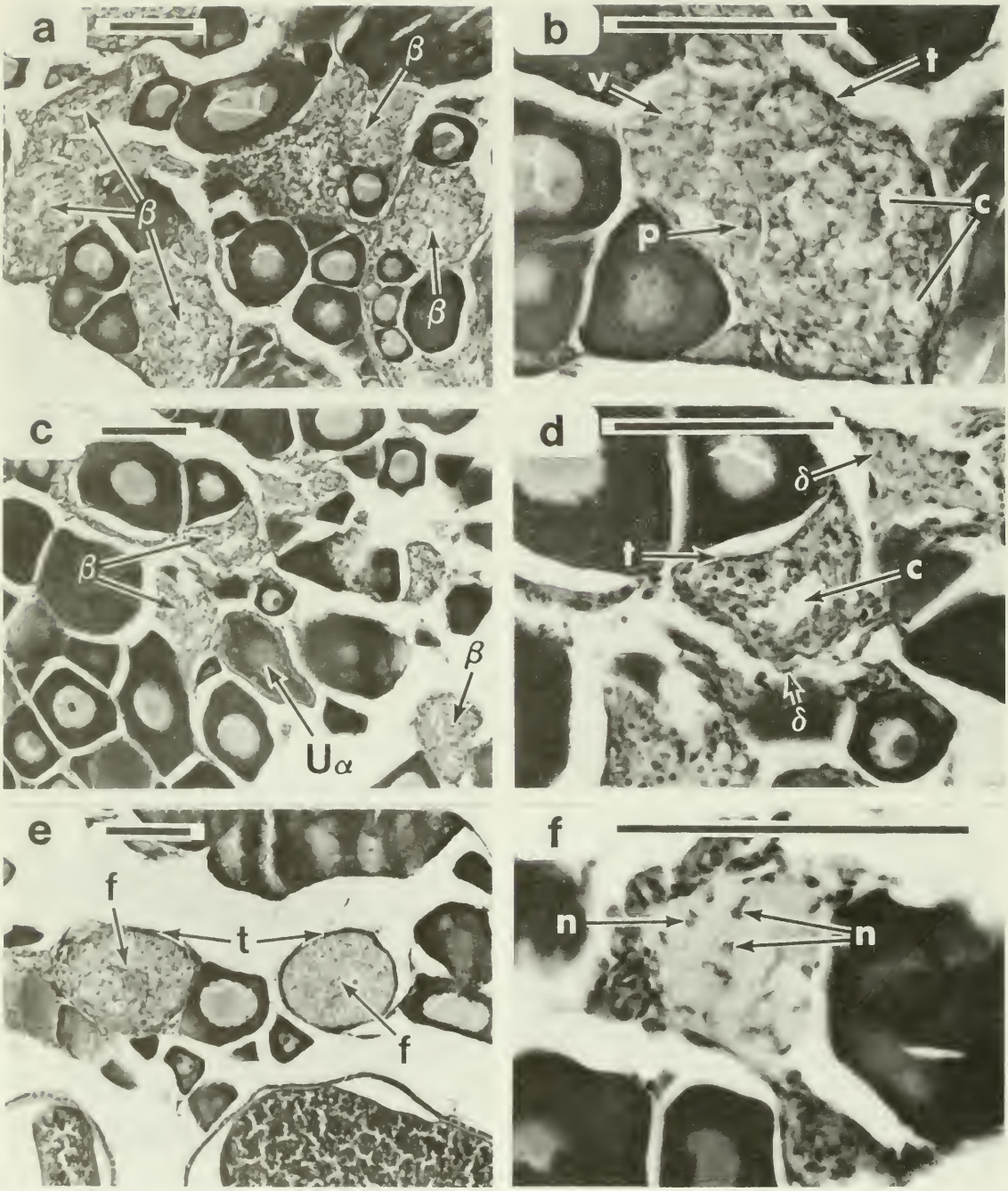

FIGURE 3.—Stages of atresia following after complete yolk absorption (bar = 0.1 mm). a) and b) Typical beta (β) stage atresia. Note the disorganized granulosa cells with some pycnotic nuclei (p) or intracellular vacuoles (v) (t = outer layer of thecal cells, c = intercellular cavities). c) and d) Disintegration of granulosa continues in these older beta (β) stage atresia. Note the large intercellular cavity (c) and the prominent, contracted thecal cell layer (t). Also present is an unyolked oocyte in early alpha ($U\alpha$) stage and several delta (δ) stage atresia cells. e) Two types of gamma (γ) atresia seen in northern anchovy ovaries. Note flocculent material (f) and the thecal layer (t). f) Delta (δ) stage atresia characterized by dark yellow fine granular pigment and an irregular nucleus (n).

TABLE 1.—Percentage of northern anchovy females with ovaries containing various levels of alpha stage atresia during starvation and after the resumption of feeding.[1]

Elapsed time from capture (d)	Feeding condition			Percentage of ovaries with levels of alpha stage atresia									
				Unyolked oocytes[2]			Partially yolked oocytes[2]			Yolked oocytes[3]			
	Starved	Fed	N	None	N ≤5	N >5	None	N ≤5	N >5	None	F <50%	F = 50-90%	F ≥91%
3	X		24	79	13	8	46	29	25	50	33	0	13
6	X		21	19	14	67	14	14	62	5	10	19	48
9	X		24	12	17	71	0	58	34	0	8	17	42
13	X		20	10	15	75	20	15	20	0	0	5	40
16	X		24	0	12	88	4	17	17	0	0	0	8
20	X		22	0	36	64	0	0	4	0	0	0	4
23	X		23	9	39	52	0	4	13	0	0	0	0
27	X		23	4	57	39	0	0	0	0	0	0	0
34		X	23	70	17	13	4	0	0	0	0	0	0
41		X	18	83	17	0	17	0	0	17	0	0	0
62		X	22	90	5	5	64	9	9	36	23	0	0

[1]Feeding begins on the 28th day.
[2]N = mean number of atretic oocytes per 6 μm section.
[3]F = mean percentage of atretic oocytes per 6 μm section.

TABLE 2.—Percentage of northern anchovy females with ovaries containing various levels of beta and gamma+delta stage atresia and yolked oocytes during starvation and after the resumption of feeding.[1]

Elapsed time from capture (d)	Feeding condition			Percentage of ovaries with levels of atresia									Oocyte types	
				Beta stage atresia[2]			Beta stage atresia with no yolked oocytes[2]			Gamma+delta stage atresia[2]			Yolked oocytes present	Only partial and unyolked oocytes present
	Starved	Fed	N	None	N ≤5	N >5	None	N ≤5	N >5	None	N ≤5	N >5		
3	X		24	71	21	8	0	4	0	92	4	4	96	4
6	X		21	24	24	52	0	5	14	71	24	5	81	19
9	X		24	4	8	88	0	0	33	88	8	4	67	33
13	X		20	0	15	85	0	10	45	60	25	15	45	55
16	X		24	0	12	88	0	12	79	16	46	38	8	92
20	X		22	0	9	91	0	9	86	9	36	55	4	96
23	X		23	0	17	83	0	17	83	13	26	61	0	100
27	X		23	0	44	56	0	44	56	26	35	39	0	100
34		X	23	35	48	17	35	48	17	4	13	83	0	100
41		X	18	88	6	6	78	0	6	0	28	72	17	83
62		X	22	82	18	0	35	5	0	0	50	50	59	41

[1]Feeding begins on the 28th day.
[2]N = mean number of atretic follicles per 6 μm section.

resorption (Fig. 4). None of the females sampled on the 23d day had yolked oocytes, indicating that all yolked oocytes had passed through the alpha stage of atresia by this time.

The resorption of unyolked and partially yolked oocytes began just as rapidly as did the resorption of yolked oocytes. The percentage of females with atretic unyolked oocytes in the alpha stage increased sharply from 21% on the 3d day of starvation to 90% on the 13th day. Throughout the rest of the 27-d starvation period nearly all of the females (90-100%) had some unyolked oocytes in the alpha stage of atresia, indicating a continual recruitment of atretic follicles from the unyolked and partially yolked oocyte classes. Thus, alpha stage unyolked and partially yolked oocytes are present in regressing ovaries for a much longer period than is the alpha stage of yolked oocytes. This difference probably is due to the greater number of unyolked and partially yolked oocytes in mature ovaries. Yolked oocytes constitute <1% of the total number of oocytes present in mature ovaries.

The incidence of beta stage atretic follicles also increased sharply over the first 9 d of the starvation period and followed a pattern similar to that described for the incidence of alpha atresia from unyolked eggs (Fig. 4). After attaining a high value on the ninth day the incidence of beta atresia remained high until the end of the starvation period as atretic follicles from yolked and unyolked oocytes degraded from the alpha to the beta stage of atresia. Incidence of gamma+delta stages (the third and fourth stages of follicle degeneration) increased later than did alpha and beta stages and remained high after the onset of feeding.

Once feeding resumed (day 28), rapid resorption of yolked and unyolked follicles ceased and the

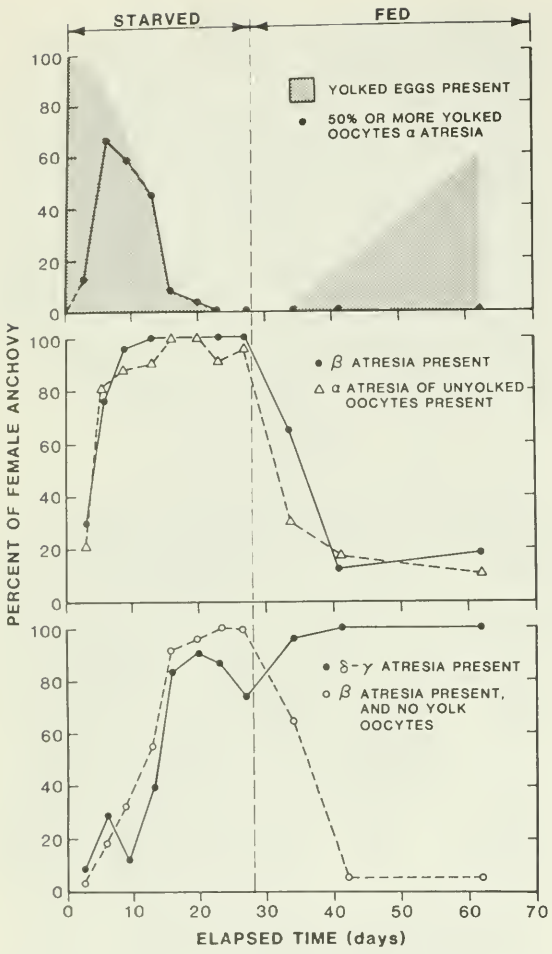

FIGURE 4.—Percentages of captive female northern anchovy with ovaries having various atretic characteristics during a 27-d starvation period and after the onset of feeding. Each percentage is calculated from a sample of 18-24 females (see Tables 1 and 2); alpha, beta, and gamma through delta stages of atretic follicles are those defined by Bretschneider and Duyvene de Wit (1941).

dominant process became maturation rather than resorption. This was indicated by sharp declines in the percentages of females with alpha stage atresia of unyolked oocytes and beta stage atretic follicles, and the reappearance of yolked oocytes (day 41). After only 1 wk of feeding the percentage of females with alpha stage atresia from partially unyolked oocytes dropped from 96 to 30%.

Some inferences can be drawn from these data regarding the duration of atretic stages. The sharp and simultaneous decline in beta stage atretic follicles and alpha stage atresia of unyolked oocytes (following the onset of feeding) indicates that alpha and beta stages must have a short and similar duration. The duration of alpha and beta atresia probably is <2 wk, since the incidence of these two stages dropped to very low levels 2 wk after the onset of feeding; a lag of about 1 wk existed between the first high incidence of females with beta atresia (9 d) and that for gamma+delta (16 d), indicating that the duration of the beta stage may be about 1 wk. The continued high incidence of gamma+delta stages of atretic follicles long after the onset of feeding indicates that these late atretic stages must persist in the ovary for much longer periods than alpha or beta stages. Although gamma+delta stages were present in all ovaries on the last day of the experiment their abundance within an ovary had decreased indicating that even the delta stage would eventually disappear, eliminating the last histological sign of past reproductive activity. We conclude from these inferences that the alpha and beta stages persist in the ovary for 1 wk or less whereas gamma+delta stages persist for over a month, but eventually all signs of past reproductive activity are lost.

The occurrence of alpha stage atresia of yolked oocytes is the best characteristic to use to back-calculate the time of past reproductive activity in field-caught specimens because the stage is of relatively short duration and the time required to resorb all yolked oocytes is relatively short. On the other hand, alpha stage atresia of unyolked oocytes, and beta and gamma+delta stages are less useful for back-calculations because these stages may occur in an ovary for extended periods while atretic oocytes are recruited from the large reservoir of unyolked oocytes in the ovary. In addition, estimates of the time since the onset of atresia in ovaries without yolked oocytes (using the incidence of beta or gamma+delta atretic stages) will always be uncertain because atresia of unyolked oocytes may occur at low levels in immature or developing ovaries as well as in regressing ovaries.

For the laboratory specimens, we calculated the average elapsed time from the onset of ovary resorption using various classes of alpha stage atresia of yolked oocytes and beta atresia in ovaries without yolked oocytes (Table 3). We prefer the criteria of 50% or more of the yolked oocytes with alpha stage atresia because it is likely that no spawning will occur in such females. The average duration of this stage (alpha, yolked, ≥50%) in the starving laboratory females was about 9 d and ranged from <3 to 20 d from the onset of starvation.

Starvation may have induced a higher rate of

TABLE 3.—Mean and maximum duration of various atretic characteristics of the ovaries of starved northern anchovy.

Atretic characteristics	Mean duration (d)	Maximum duration (d)
Alpha atresia of yolked oocytes present	8.0	20
Alpha stage atresia in:		
<50% of yolked oocytes	4.5	9
50-90% of yolked oocytes	8.1	13
91% or more of yolked oocytes	9.3	20
50% or more of yolked oocytes	9.0	20
No yolked oocytes present and beta atresia present	>16	>27

oocyte resorption than usually occurs under natural conditions. Variation in the female nutritional state, food ration, water temperature, day length, and a host of other variables may affect rates of atresia. In addition, field data indicate (see next section) that some spawning may occur in females with low to moderate levels of alpha (yolked) atresia, indicating that such stages may persist under natural conditions for extended periods. Despite these uncertainties we believe that our laboratory estimates of atretic rates are useful for making a rough estimate of the minimum time elapsed since the end of the spawning season in sea-caught females.

Natural Rates of Atresia

In this section we analyze sea data taken since 1977 for the occurrence of four ovarian atretic states in a northern anchovy population:

Atretic state 0—no alpha atresia of yolked oocytes (yolked oocytes present).

Atretic state 1—alpha atresia of yolked oocytes where <50% of the yolked oocytes are affected.

Atretic state 2—alpha atresia of yolked oocytes where 50% or more of the yolked ooctyes are affected (Fig. 5a, b).

Atretic state 3—ovaries with no yolked oocytes present and beta stage atresia present (Fig. 5c).

In addition to the atretic condition of the ovary, we also include histological evidence of recent or imminent spawning using the system of Hunter

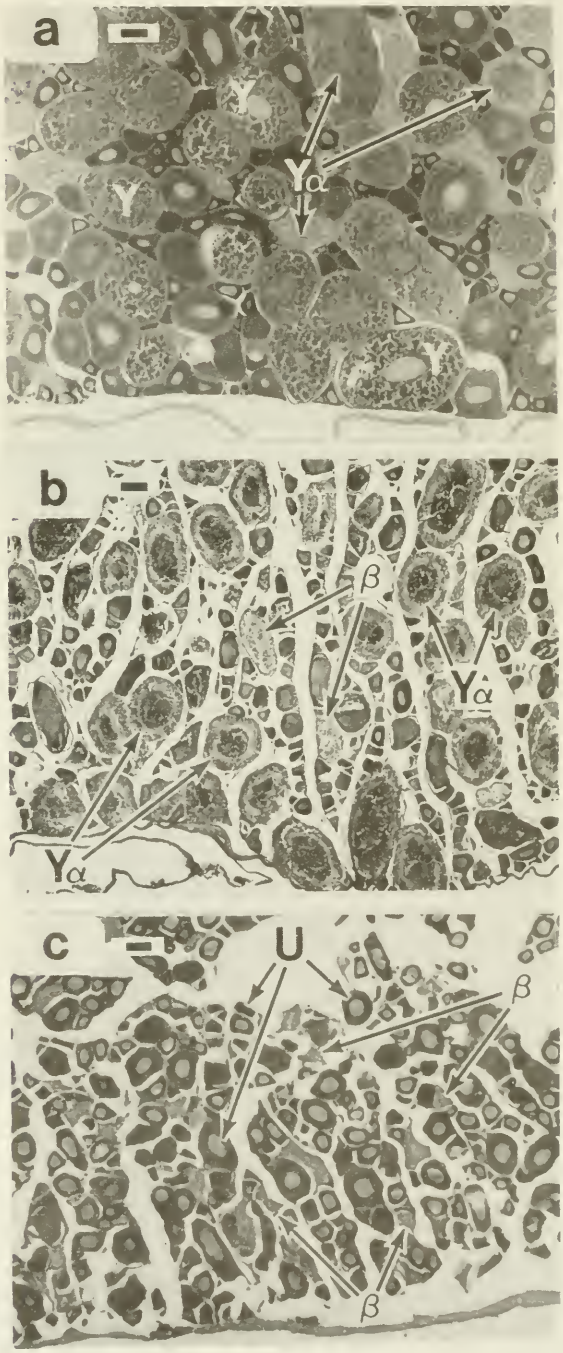

FIGURE 5.—Northern anchovy ovaries with increasing atresia states (bar = 0.1 mm). a) 50% of all yolked oocytes (Y) are in an alpha (α) stage of atresia (both early and late are counted). This is the division point between atretic state 1 and atretic state 2. b) 100% (all) yolked oocytes are in an alpha stage of atresia ($Y\alpha$). Also present are a few unyolked alpha atretic oocytes and several beta (β) stage atretic follicles. This is still in atretic state 2. c) All yolk has been resorbed leaving only unyolked oocytes (U) and many beta (β) stage atretic follicles. This is atretic state 3.

and Goldberg (1980), i.e., presence of hydrated eggs (imminent spawning), day 0 or new postovulatory follicles (spawning on the night of capture), and 1-d-old postovulatory follicles (spawning on the night before capture). We also include the number of females judged to have inactive or immature ovaries with no evidence of atresia. All data on the incidence of reproductive states are given in Table 4. In the discussion that follows we select and regroup these data in various fashions to test hypotheses and document trends.

Incidence of Spawning in Atretic Females

An important assumption underlying interpretation of ovarian atresia is that the spawning season has or is going to cease, in other words, the probability of spawning in females with atretic ovaries would be expected to be low. To test this assumption we selected from Table 4 the females which had alpha stage atresia of yolked oocytes (atretic states 1 and 2) or yolked oocytes without alpha atresia (atresia state 0) and calculated the percentage of these females that had hydrated oocytes, new (day 0) postovulatory follicles, and 1-d-old postovulatory follicles. Of the females classed in atretic state 1 (females with <50% of the yolked oocytes in alpha stage of atresia), 14% showed evidence of recent or imminent spawning (postovulatory follicles or hydrated oocytes); 29% of the females without atresia showed evidence of spawning (Table 5). Only 1% of those in atretic state 2 (females 50% or more atretic yolked oocytes) had recently been reproductively active. That 1.8% of females in atretic state 1 had hydrated eggs and 3.7% had age 0 d postovulatory

TABLE 4.—Numbers of female northern anchovy in various atretic and reproductive states northern California

Collection dates number of mature females/collection	Atretic state[1]	Hydrated oocytes	Postovulatory follicles		Yolked oocytes	No yolked oocytes	Immature no histology[4]	Total
			0 day[2]	1 day[3]				
1977	0	1	2		13	4		20
09/09-09/10	1							0
	2							0
(10)	3					3		3
	x	1	2	0	13	7	0	23
1978	0				1			1
05/07-05/11	1			1	5			6
	2				4			4
(10)	3					6		6
	x	0	0	1	10	6	0	17
1979	0	39	44	52	279	89	110	613
01/26-02/16	1			1				1
	2				1			1
(10)	3					2		2
	x	39	44	53	280	91	110	617
1979	0	16	51	45	284	27	18	441
03/22-04/14	1		1	5	36			42
	2				6			6
(10)	3					16		16
	x	16	52	50	326	43	18	505
1979	0			1	8	4		13
06/09-06/19	1				3			3
	2				1			1
(12)	3					16		16
	x	0	0	1	12	20	0	33
1979	0				9	31		40
09/19-09/23	1							0
	2				5			5
(10)	3					25		25
	x	0	0	0	14	56	0	70
1980	0	25	72	52	241			390
03/20-04/10	1				9			9
	2				1			1
(20)	3					2		2
	x	25	72	52	251	2	0	402
1980	0		4	9	63	8	6	90
04/24-04/27	1				11			11
	2				14			14
(20)	3					63		63
	x	0	4	9	88	71	6	178

[1] Atretic state 0 = no alpha stage atresia of yolked oocytes.
state 1 = alpha stage atresia of yolked oocytes present but < 50% oocytes affected.
state 2 = alpha stage atresia of yolked oocytes present, 50% or more oocytes affected.
state 3 = no yolked oocytes present and beta stage atresia present.

follicles indicate that some of the females in atretic state 1 spawn despite the atretic condition of their ovaries. On the other hand, only two females classed in atretic state 2 had a recent history of spawning. These two females had few yolked oocytes remaining, all but one was in alpha atresia. This atresia may have increased or even started during the time elapsed between hydration and capture. In short, the females in atretic state 2 probably did not spawn in the highly atretic state in which they were captured. No doubt exists that females with moderate levels of ovarian atresia are capable of spawning because they often are hormonally induced to do so in the laboratory. In summary these data indicate that significant numbers of females in atretic state 1 may continue to spawn under natural conditions, although the probability of spawning appears to be about half that of fish without ovarian atresia. Few or none of the females in atretic state 2 continue to spawn indicating that this stage is probably the best one to use to calculate cessation of spawning in the population.

Forcasting the end of Spawning Using Ovarian Atretic States

In our laboratory study atretic state 1 had an average duration of about 5 d and atretic state 2, 9 d; state 3 was in excess of 16 d and probably persists for 30 or more days (Table 3). In the sea, linear projections of the end of the spawning season from early incidence of atresia is not realistic since the numbers of females with regressing ovaries would be expected to increase sharply at the end of the season.

listed in order of collection dates for southern and Baja California (1977-82) and for (1979, 1982).

Collection dates number of mature females/collection	Atretic state[1]	Hydrated oocytes	Postovulatory follicles		Yolked oocytes	No yolked oocytes	Immature no histology[4]	Total
			0 day[2]	1 day[3]				
1980	0			3	32	11		46
05/15-05/28	1		1		5			6
	2				2			2
(20)	3					16		16
	x	0	1	3	39	27	0	70
1981	0	119	122	148	862	58		1,309
02/05-03/06	1		2	1	19			22
	2				3			3
(15)	3					10		10
	x	119	124	149	884	68	0	1,344
1981	0	77	96	113	559	7		852
04/01-04/19	1		3	2	57			62
	2		1		45			46
(15)	3					19		19
	x	77	100	115	661	26	0	979
1981	0		2	1	7			10
04/15-04/30	1				5			5
	2				8			8
(15)	3					7		7
	x	0	2	1	20	7	0	30
1982	0	104	101	189	1,172	52	8	1,626
01/28-03/08	1	2	2	10	32			46
	2				2			2
(15)	3					6		6
	x	106	103	199	1,206	58	8	1,680
1979[5]	0		1		42			43
03/20-03/22	1		1		40			41
	2				41			41
(30)	3					25		25
	x	0	2	0	123	25	0	150
1982[5]	0	2			27	2	11	42
01/22-01/25	1	3		2	14			19
	2			1	5			6
(15)	3					13		13
	x	5	0	3	45	16	11	80

[2]New postovulatory follicles <24 h old.
[3]Postovulatory follicles about 24 h old.
[4]Female not examined histologically, ovary ≤1% of body weight.
[5]Female northern anchovy from northern California; rest of females were from southern and Baja California.

TABLE 5.—Percentage of northern anchovy females taken from 1977 to 1982[1] that were classed in three atretic states that occurred in each of five reproductive classes.

	Reproductive state						
			Postovulatory follicles				
Atretic state	Percent yolked oocytes with alpha stage atresia	Hydrated oocytes (%)	0 day (%)	1 day (%)	Spawning recent or imminent[2] (%)	No evidence of recent spawning[3] (%)	Total number of females
0	0	7.5	9.7	12.0	29.3	70.7	5,090
1	<50	1.8	3.7	8.1	13.6	86.4	273
2	≥50	0	0.7	0.7	1.4	98.6	140

[1]Calculated from data given in Table 4; only females with yolked oocytes are considered.
[2]Females with either hydrated oocytes or postovulatory follicles ages 0 or 1 d (the sum of the first three columns).
[3]Females with yolked oocytes but without hydrated oocytes or postovulatory follicles.

This nonlinearity becomes obvious when the end of the spawning season is extrapolated from numbers of females classed in atretic state 2. For example, of the 1,620 mature females taken during the peak of spawning (28 January-18 March 1982) in southern California (Table 4), only two were in atretic state 2 and 1,612 had yet to pass through state 2. Since laboratory data indicate that about 9 d are required to pass through atretic state 2, it would require $(1{,}612/2) \times 9$, or over 7,000 d for the entire population to become atretic at the rates of atresia observed in February, which, of course, is nonsense. Projections of the end of the spawning season using higher rates of atresia taken in April in southern California (24-27 April 1980) give a more realistic projection $((87/14) \times 9 = 56$ d). Such an arithmetic projection may be inappropriate for collections which have a very high rate of atresia such as those taken in Monterey in March 1979 ($(84/41) \times 9 = 18$ d), and a geometric model might be preferable. The point we wish to emphasize is that atretic rates are nonlinear over the season with the rate increasing markedly as the season closes. Thus only samples taken near the close of the spawning season are of value for forecasting the end of spawning for the population.

Seasonal Changes in Atresia Among Females of Different Lengths

To evaluate how atretic rates change among females of different lengths, we segregated our data into two length classes (females ≤10 cm SL and those >10 cm SL) and calculated the percentage of mature females that had atretic ovaries (atretic states 1-3 combined). Mature is defined here as all females except those which have yet to reach first maturity (small females with small immature non-atretic ovaries). We also calculated the fraction of females in each length class with 1-d-old postovulatory follicles, a measure of the percentage of females spawning daily (Hunter and Goldberg 1980).

In every case, regardless of cruise or season, small females (≤10 cm SL) consistently had a higher rate of ovarian atresia than did larger ones (>10 cm SL) (Table 6). This is a strong trend as the probability of such an event (9 pairs of the same sign) is $(1/2)^9$. In addition, the difference between pairs was statistically significant (chi-square test) even when the levels of atresia were quite low. For example, in February-March 1981, only 4.1% of the small females and 1.9% of the large females were atretic, yet this difference was significant at $P < 0.05$ using the chi-square test. As would be expected, the percentage of females with atretic ovaries increased in both length classes as the season progressed from January through June.

The consistency of the differences in the incidence of atresia between large and small females indicates that the smaller ones must have a much shorter spawning season than larger ones. Females <10 cm long are typically about 1-yr-old and are in their first spawning season whereas those longer than 10 cm are predominantly 2-3 yr old and have spawned during the previous seasons. These data indicate that the first spawning season of females may be quite short with significant numbers of females leaving the spawning population in early April, while the older fish continue to spawn. That the rates of atresia in young fish were always higher even in the peak months of spawning such as February and March indicates that a small percentage of small females may only spawn a few times during the season in contrast to the older females which appear to be spawning at about weekly intervals for months. The fraction of small females spawning per day would be expected to be less than larger females since the small females have a higher incidence of ovarian atresia. We calculated the fraction of females spawning per

TABLE 6.—Percentage of mature northern anchovy females in two length classes with atretic ovaries. Females from north of Point Conception and groups with fewer than nine females per length class excluded.

Cruise period			Number of mature females[1]		Percent of mature females with atretic ovaries[2]		Fraction mature females spawning per day percent[3]	
From	to	year	≤10 cm	>10 cm	≤10 cm	>10 cm	≤10 cm	>10 cm
01/26	→02/16	1979	121	297	1.7	0.7	8.0	15.9
01/28	→03/18	1982	97	1,523	14.6	2.6	14.1	12.2
02/05	→03/06	1981	462	824	4.1	1.9	10.2	13.7
03/20	→04/10	1980	68	334	8.8	1.8	11.7	15.2
03/22	→04/14	1979	30	430	23.3	13.3	3.8	11.8
04/01	→04/19	1981	102	870	39.2	10.0	10.5	12.9
04/24	→04/27	1980	64	100	96.9	26.0	0	8.6
04/15	→04/30	1981	10	20	80.0	60.0	0	5.3
05/15	→05/28	1980	15	44	73.3	29.5	6.2	4.4

[1] All females given in Table 4 except those with immature ovaries and those not examined histologically.
[2] All females in atretic states, 1, 2, and 3 combined.
[3] Fraction of females spawning = F, where $F = \frac{m_{1i}}{2m_{1i} + m_{ni}}$

m_{ni} = mature nonspawning females, and m_{1i} = females with 1-d-old postovulatory follicles.

day for the two length classes to test this assumption. We used the Stauffer and Picquelle (footnote 3) method for estimating spawning fraction as it corrects for biases in the numbers of females with hydrated eggs, i.e.,

$$F = \frac{M_{1i}}{2M_{1i} + m_{ni}}$$

where F = fraction of females spawning per day, M_{1i} = number of females with 1-d-old postovulatory follicles, and m_{ni} = number of mature females with no recent spawning history (females with postovulatory follicles or hydrated eggs are excluded). Examination of Table 6 indicates that differences in spawning fraction between the two size classes of females were much less distinct than were the differences in ovarian atresia. Using only the 8 cruises in which the numbers of females in each of the two length classes exceeded 10, the mean difference in spawning fraction (fraction for large females − fraction for small females) for the set of 8 cruises was +3.76% with 95% C.I. ±3.50% indicating a small difference in spawning frequency between the two length classes that is just barely significant at the 5% level. We believe the reason that differences in atretic fraction between large and small females are much more consistent than those in spawning fraction is that spawning fraction has a greater variability and a much more limited dynamic range than does the atretic fraction. Spawning fraction varies from 0 to about 16% and may be affected by time of day and schooling behavior (Hunter and Goldberg 1980). Atretic fraction varies from 0 to nearly 100%, is not linked to reproductive behavior, and consequently, is probably not affected by time of day or schooling.

DISCUSSION

Evaluation of Atretic Classification

Our objective was to evaluate the use of ovarian atretic states to characterize the reproductive biology of northern anchovy populations. We included in our analysis of laboratory data many atretic characteristics not used to construct the three atretic states utilized in the analysis of sea data. These additional characters could be used to create additional states or to more precisely delimit the existing ones. Our selection of characteristics was based in part on ease of identification since for population work thousands of histological sections were examined. Other considerations include the fact that statistical analysis indicated that classifiers frequently confused beta stage atretic follicles in yolked ovaries with postovulatory follicles older than 24 h, and, as a consequence, beta atresia was not used as a diagnostic character in ovaries with yolked oocytes. Alpha stage atresia was the most useful atretic stage because the type of oocyte (yolked) undergoing atresia is still discernible. In addition, alpha stage atretic oocytes can be easily distinguished from postovulatory follicles whereas this is not the case for later atretic stages.

Three atretic states were defined and applied to sea data. The incidence of all three atretic states combined was a sensitive index of the reproductive state of the population over the spawning season.

In fact, the atretic condition of the ovary was a more sensitive index of seasonal changes in the reproductive rate among size classes of females than was the incidence of spawning based on the presence of postovulatory follicles.

Atretic state 1 (<50% of yolked oocytes in the alpha stage of atresia) was not useful for estimating atretic rates in an absolute sense since this state appeared to persist in natural populations for extended and probably variable periods. Some spawning occurred among females classed in atretic state 1, although the frequency of spawning was less than half of that of females without ovarian atresia. Batch fecundity might also be reduced in females classed in atretic state 1, a speculation worth further study. Atretic state 1 was a useful index of atretic rates during peak spawning months. At such times it was the most common atretic condition and detection of differences in atretic rates among length classes was largely a function of the number of females in this state.

Atretic state 2 (50% or more of yolked oocytes in alpha atresia) persisted for about 9 d in the laboratory, and judging by its low frequency in field collections this state may have a similarly short duration in natural populations. Females with ovaries in this state rarely or never spawn, as might be expected, since more than half of the yolked oocytes are not viable. In addition, a short duration of this state also might be expected on the grounds that it seems maladaptive to prolong such a threshold condition. For the above reasons atretic state 2 seems to be the best absolute measure of the rates of ovary resorption in the population and the only state that might provide an accurate forecast of the end decline of reproduction in a population. Unfortunately, accurate forecasts of the end of spawning for a population can be made only near the end of the spawning season.

Atretic state 3 (no yolked oocytes with beta atresia present) identifies females in late postspawning condition. Such females cannot be separated from immature females on the basis of gonad weight or using gross anatomical criteria. This state persisted for about 30 d in the laboratory, but it may last much longer under natural conditions while the numerous small oocytes are resorbed. The laboratory data indicate that the duration of this state could be increased if the definitions were changed to include gamma+delta stages of atresia which have a longer life in the ovary than the beta stage. The laboratory data also indicated that even gamma+delta stages of atresia would eventually disappear from the ovary so that no signs of previous spawning activity would exist in a regressed ovary. It is doubtful that the duration of atretic state 3 or any late postspawning state will ever be accurately estimated because it is dependent on too many environmental circumstances. Nevertheless, this state is very useful in separating females in postspawning condition from females with no previous reproductive history. This is an essential distinction for estimating spawning biomass (Stauffer and Picquelle footnote 3) and for determining the size or age at first reproduction (Hunter and Macewicz 1980).

Possibly the most important future application of atretic classification of ovaries is for process oriented sea work on the reproductive biology of multiple spawning fish such as the northern anchovy. Such work does not require a large sample as do estimates of reproductive characteristics for an entire population. The reproductive state of an individual female can be accurately defined by the atretic criteria we have discussed, and the spawning state criteria described by Hunter and Goldberg (1980). The reproductive characteristics of a female can be related to its physiological state (age, fat content, biochemical composition, and instantaneous growth rate from otoliths or RNA/DNA ratios) and functional relationships established between reproduction and the environment. In this way the factors controlling the duration of the spawning season, and the total fecundity during the season, can be identified under natural conditions.

Biological Implications

Several important biological conclusions can be drawn from this work. Only a few attempts have been made to estimate the time needed for a follicle to disappear by atresia in vertebrates and no information exists for fishes (Byskov 1978). Our focus was on atretic rates of all oocytes in the ovary and not on an individual follicle; nevertheless, the striking speed with which all yolked oocytes passed through the initial stages of atresia indicate that the rate for individual follicles must be high. Similar rates were observed in the guppy by Lambert (1970a). In the guppy, alpha stage atresia of yolked oocytes appears about 1 d after parturition, and beta stage atresia appeared about 2 d after the first alpha stages were detected; beta stages persisted for only 11 d. In the anchovy, the average time for all yolked oocytes in the ovary to pass through alpha atresia was 8.0 d and the

maximum time was 29 d. Thus the effect of atresia on fecundity may be underestimated since the duration of atretic stages is short and a small standing stock of atretic oocytes could be an indication of a high loss rate. On the other hand, laboratory studies seem to indicate that atretic rates are not sufficiently high to account for the differences in fecundity observed when fish are fed high and low rations (Tyler and Dunn 1976; Wootton 1979). The duration of the atretic stages in these studies was unknown, however.

Additional evidence for the volatility of the reproductive state of anchovy is an important contribution of this study. Our laboratory data indicated that given a shortage of food the ovary can be rapidly resorbed leaving no trace of former reproductive activity in a few months or less, but when given sufficient food atresia stopped, maturation and vitellogenesis resumed, and a reproductively active ovary was rapidly reformed within 35 d. Clearly, in such multiple spawning fishes as the anchovy, more than one spawning season per year is possible given the appropriate environmental conditions. This may explain the occurrence of a second annual spawning period in the Peruvian anchoveta (Santander and Castillo 1976) and the occasional heavy fall spawning of the northern anchovy (Smith 1972). That active ovaries are consistently produced from small, inactive ones in 30-60 d in the laboratory (Leong 1971; Hunter and Leong 1981) and that some reproductively active females are found the year around also supports this view.

Food shortage does not always lead to regression of the ovary in anchovy or any other multiple spawning fishes. In addition to food ration, regression of the ovary also depends upon the level of energy reserves, the timing of the reproductive cycle, and perhaps certain environmental conditions such as temperature and day length. For example, starvation of 40-80 d did not block the initial increase in the size of ovaries of the goby *Gillichthys* at the start of the reproductive cycle in July but only 23 d of starvation resulted in ovarian regression in January when active vitellogenesis was occurring (de Vlaming 1971). Similarly we noted in a preliminary experiment that starving anchovy of 25% greater wet weight than those used in this study produced a slower regression of the ovary over a 36-d period than occurred in the present study. The present study is more representative of natural conditions since the fish were taken in midspawning season when their ovaries were active whereas in the preliminary study the fish were taken out of season and fed heavily for 30 d to induce gonad maturation before the onset of the 36-d starvation period.

Another important conclusion from this study was that young female anchovy spawning for the first time probably have a much shorter reproductive season than do older females. Hunter and Leong (1981) estimated that the average female spawns about 20 times per year. Thus the older females must spawn considerably more often than 20 times per year, and probably contribute a much larger fraction of the reproductive output of the population than a proportionate share by weight. This indicates the importance of maintaining older fish in the population and that danger may exist if older fish are overharvested.

ACKNOWLEDGMENTS

We thank Roderick Leong (Southwest Fisheries Center (SWFC)) for providing and maintaining the northern anchovy used in the laboratory study. We thank Kenneth Mais (California Department of Fish and Game) for providing some specimens. Pedro Paloma (SWFC) and Eric Lynn (SWFC) assisted in histological classifications. Carol Kimbrell (SWFC) and Susan Picquelle (SWFC) provided valuable assistance in analyzing the data.

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EGG PRODUCTION OF THE CENTRAL STOCK OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, 1951-82

NANCY C. H. LO[1]

ABSTRACT

A model was developed for estimating daily production of eggs of northern anchovy from counts of the total numbers of eggs and size-frequency distribution of larvae. Estimates of egg production using this model were compared with three estimates based on the mortality rates of staged (aged) eggs. The model was used to calculate daily egg production of anchovy for a 24-year time series (1951-82) (data were collected each year from 1951 to 1966 and 1979 to present and every 3 years from 1966 to 1979). Comparisons of this index of stock abundance with ones based on the standing stock of larvae indicate that the present model is a better index of spawning biomass. It was found from the 1979-81 data that the eggs and larvae (< 20 days) have different forms of instantaneous mortality rate (IMR): The larval IMR was age dependent, i.e., $z(t) = \beta/t$ for $t_c < t$ whereas the egg IMR was constant $z(t) = \alpha$ for $t < t_c$ where t_c is incubation time or yolk-sac absorption. Based upon this model, the daily egg production, and egg-larval mortality rates for larvae < 20 days (< 8 mm preserved length), were estimated for 1951-82 from data collected with 1 m ring nets and bongo nets. Egg production varies with stock size proportionally if the reproduction effort remains constant. The egg production is a better index of stock size than the larval abundance because the latter is subject to the inherent egg and larval mortality in addition to reproductive output.

Ichthyoplankton data have been used extensively for estimating biomass (or spawning biomass) of marine fish stocks (Murphy 1966; Ahlstrom 1968; Smith 1972). One of the tacit assumptions underlying most of the methods used for estimating biomass from ichthyoplankton data is that egg or larval mortality is constant among years. In recent years, however, it has become increasingly evident that egg and larval mortality is quite variable among years and among life stages (Ahlstrom 1954; Marr 1956; Colton 1959; Burd and Parnell 1972; Cushing 1973; Fager 1973; Harding and Talbot 1973). As a result, biomass indices based on standing stock of eggs or larvae are subject to a considerable bias if the interannual variability in mortality is not taken into account. In order to eliminate the bias, attempts were made to estimate the spawning biomass by using the egg production and reproduction parameters (Saville 1964; Beverton and Holt 1965; Ciechomski and Capezzani 1973). The basic model is

$$P_0 = B_a R(E/W) \qquad (1)$$

where P_0 = egg production at age zero,
B_a = spawning biomass,
R = proportion of spawning biomass being female,
E = average batch fecundity,
W = average mature female weight.

Equation (1) is adequate for species that spawn only once during a season. But for the multiple spawners, like northern anchovy, *Engraulis mordax*, one needs to include another adult parameter, the proportion of mature spawning female (F), in the equation (Parker 1980). Moreover, Parker chose to use egg production per day, as this could be easily estimated from a single cruise. Thus, the egg production model (EPM) for northern anchovy (or any multiple spawning stock) becomes

$$P_0 = B_a R \cdot F(E/W). \qquad (2)$$

Staged eggs are used to estimate the daily egg production (number of eggs per day) of the population (P_0) while adult fish are sampled to estimate the number of eggs produced per fish weight (E/W), sex ratio (R), and proportion of mature spawning female (F). This method is, without doubt, the best of all ichthyoplankton biomass estimation techniques. It is, however, a data rich method requiring both ichthyoplankton and adult sampling plus staging of eggs and various laboratory measurements which may not be available. In this report, I present an alternative method for

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted April 1984.
FISHERY BULLETIN: VOL. 83, NO. 2, 1985.

estimating biomass using conventional ichthyoplankton data rather than the extensive sets of specialized information required by the EPM method. This alternative method provides estimates of the daily egg production (P_0) and is referred to as the historical egg production (HEP) to distinguish it from the current EPM. This model for HEP requires only the standing stock of unstaged eggs, and the numbers of larvae in various length classes subsequently transformed into age classes using Gompertz growth curve (Zweifel and Hunter[2]; Methot and Hewitt[3]; Lo 1983). Daily egg production varies proportionally with the stock size if the reproduction effort of the population remains constant. The production of eggs by a stock is certainly a better index of stock size than the standing stock of larvae (Smith 1972) because both egg and larval mortality rates are considered in the former case.

In addition to development of the model, I provide a time series of northern anchovy HEP for 1951-82. This historical record of daily egg production rather than the EPM (Equation (2)) was used to estimate anchovy biomass for these past years because data were not available for all the female reproductive parameters until 1980 and none of the eggs have been staged. It would be unpractical and take years to do all the staging of eggs that would be required for all the years. The HEP is an unbiased index for the spawning biomass (B_a) of the anchovy population for those years if the annual reproductive output per fish weight has remained constant. I do not have sufficient data to validate the assumption of constant reproductive output although 1981-82 data do indicate so.

ASSEMBLY AND BIAS CORRECTION OF EGG AND LARVAL DATA

The northern anchovy spawning area lies off central and southern California and Baja California. The sampling area was divided into 23 regions covering 17.556×10^{11} m^2 (Fig. 1). The central anchovy stock is enclosed by eight regions (4, 5, 7, 8, 9, 11, 13, and 14) with a total of 5.703×10^{11} m^2 (Duke 1976[4]; Huppert et al. 1980). Because the peak spawning season of northern anchovy was usually February-April, daily egg production for the central stock northern anchovy was computed from egg and larval data (CalCOFI[5]) collected in January-April within these eight regions. The CalCOFI survey was conducted each year until 1966 after which the survey was conducted every 3 yr. Owing to various improvements in the design of the plankton nets over the past 20 yr (Smith and Richardson 1977; Stauffer and Picquelle 1980[6]), different calibration factors were necessary to standardize the catch of eggs and larvae taken in different nets: A 1 m ring net with 0.55 mm silk mesh was used until 1969 when it was replaced by a 1 m ring net with 0.505 mm nylon mesh; this net was used until 1978 when it was replaced by the bongo net of 0.505 mm nylon mesh. Beginning in 1979, a vertical tow of the 0.333 mm mesh, 25.23 cm diameter CalVET net (CalCOFI vertical egg net) (Hewitt 1983) was used along with the 0.505 mm mesh bongo net to collect egg and larval samples in order to estimate the northern anchovy spawning biomass using the egg production method (EPM) (Parker 1980). In addition to the bias in catch caused by the different mesh sizes, biases also existed due to avoidance of the net, water volume filtered through the net (measured by water flowmeter readings), growth rate of larvae, temperature dependent incubation time (in days), and proportion of larvae from each plankton sample sorted (Zweifel and Smith 1981; Lo 1983). All data (counts of eggs and larvae) were adjusted for the above biases, when it was appropriate, following the procedures outlined by Zweifel and Smith (1981).

Egg Data

The counts of unstaged eggs from each tow were adjusted to a standardized volume of water filtered per unit depth (0.05 m^3/1 m depth = 0.05 m^2 sea surface area = area sampled by the CalVET net). The adjusted egg counts per 0.05 m^2 sea surface area were then stratified by CalCOFI regions. A weighted mean egg count per 0.05 m^2 was computed as

[2]Zweifel, J. R., and J. R. Hunter. Unpubl. manuscr. Temperature specific equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval stages.

[3]Methot, R. D., and R. P. Hewitt. 1980. A generalized growth curve for young anchovy larvae; derivation and tabular example. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-80-17, 8 p.

[4]Duke, S. 1976. CalCOFI station and region specifications. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-76-3, 37 p.

[5]CalCOFI. California Cooperative Ocean Fisheries Investigation, a program sponsored by the State of California. The cooperating agencies in the program are California Department of Fish and Game, National Marine Fisheries Service, and Scripps Institution of Oceanography, University of California.

[6]Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of central subpopulation of northern anchovy. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-80-09.

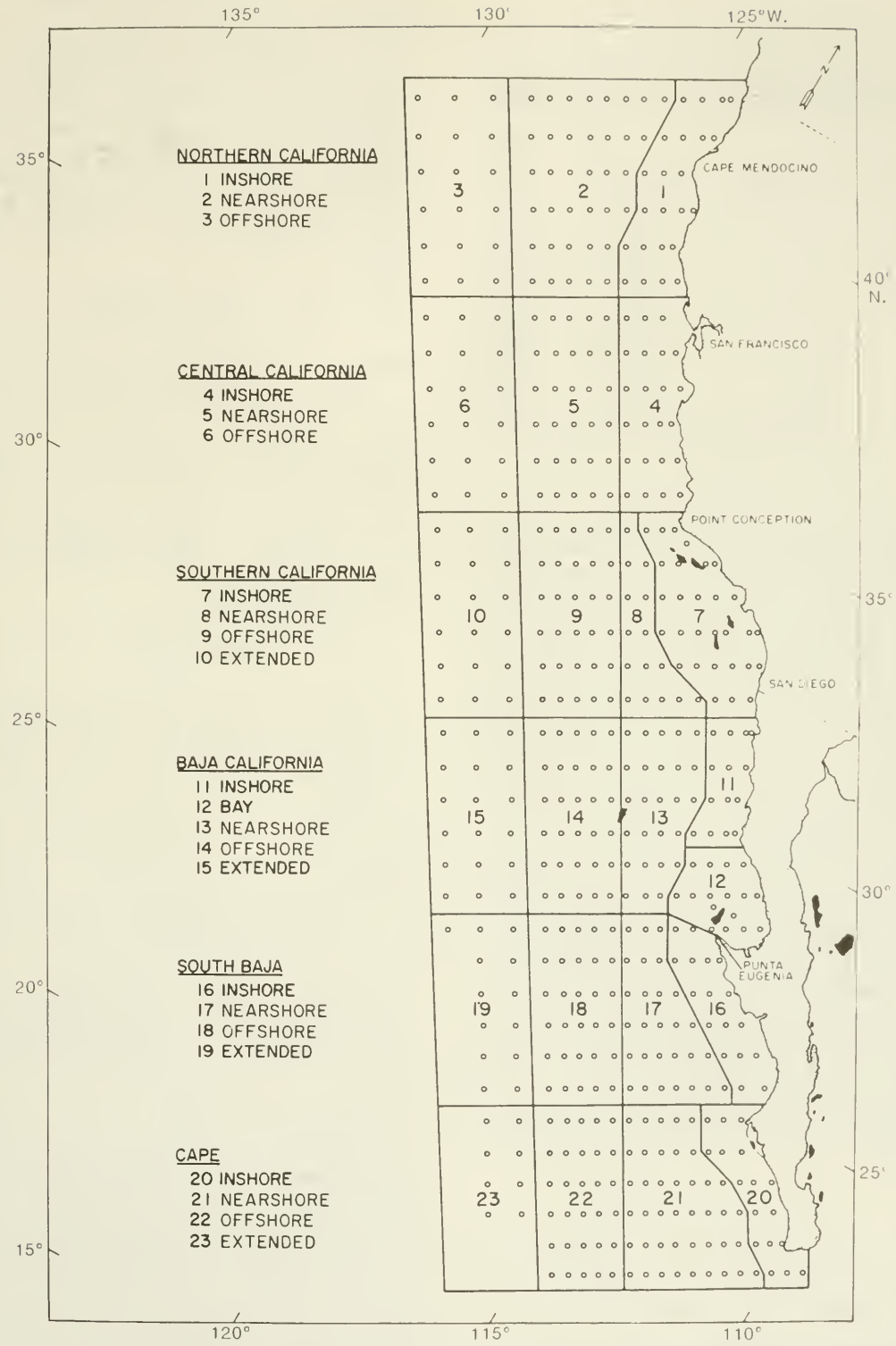

FIGURE 1.—Sampling area for estimating northern anchovy spawning biomass with CalCOFI sampling stations denoted by the open circles, and CalCOFI regions denoted by numbers (from Duke text footnote 4).

$$\bar{x}_w = \sum_i \bar{x}_i W_i, \quad \sum_i W_i = 1$$

where $\bar{x}_i$ is the adjusted mean egg count for region i and W_i is the relative area weight for region i.

Region	$nmi^2 \times 10^{-3}$	$m^2 \times 10^{-10}$	W_i
4	18	6.105	0.107
5	29	9.878	0.174
7	20	6.896	0.119
8	12	4.116	0.072
9	29	9.878	0.174
11	9	3.171	0.0538
13	21	7.122	0.126
14	29	9.866	0.174
Total	167	[1]57.031	1.00

[1]Sum is not equal to the total due to rounding error.

Zero catch was assumed for regions where no samples were taken because historical records show those regions usually had low densities of eggs and larvae. The weighted $\bar{x}_w$'s were also corrected for extrusion through the mesh by multiplying the catch by the ratio of the catch in a 0.150 mm CalVET net to the catch in the net used in a particular survey (r): $r = 3.6$ for 0.55 mm mesh silk 1 m ring net (1951-68), $r = 3.04$ for 0.505 mm mesh Nitex[7] 1 m ring net (1969-76), $r = 12.76$ for 0.505 mm mesh Nitex bongo net (1978-present) (Lo 1983). The 0.505 mm mesh bongo net seems to catch 4 times that of a 1 m ring net. The reason is unknown. (A field experiment was conducted in April 1983 to reestimate the extrusion rate of anchovy eggs from 0.505 mm mesh bongo net. The data have not been analyzed at the time of writing. Although the egg samples from bongo nets were used to compute the HEP, the bongo net is primarily used for catching anchovy larvae, whereas the CalVET net is the egg sampler. The discrepancy between bongo and 1 m ring net is not of major concern for the current anchovy biomass estimation.) The standing stock of eggs per 0.05 m^2 is then

$$m_{tI} = \bar{x}_w \cdot r$$

and

$$\text{var}(m_{tI}) = \text{var}(\bar{x}_w) r^2 + \bar{x}_w^2 \text{var}(r)$$

where m_t is the standing stock of eggs (and larvae) up to age t days from fertilization. Here t_I is the duration of incubation.

The size of standing stock of eggs depends on not only egg production rate and mortality rate but also the duration of incubation (or the incubation time), which is a function of sea temperature. The average temperature for all positive egg tows (tows which contain one or more anchovy eggs) over January-April in each year was used to estimate incubation time (t_I) using the equation (Lo 1983)

$$t_I = (18.73\, e^{-0.125\,\text{temp}})$$

where t_I = incubation time in days,
temp = temperature in degrees centigrade.

Both the standing stock of eggs (m_{tI}) and the incubation time (t_I) are essential in computing the time series of daily egg production. The temperature in January-April ranges from 11° to 19°C. The long-term average temperature from January to April is 14.25°C, thus the average incubation time is 3.15 d.

Larval Data

The anchovy larvae from all years were measured to the nearest 0.5 mm preserved length. For the purpose of estimating mortality rate, larval data were grouped into 2.5 mm, ranging 2-3.0 mm; 3.75 mm, 3.5-4.0 mm; 4.75 mm, 4.5-5.0 mm;...for larvae ≤ 30 mm. Each preserved length was first converted to a live standard length using a shrinkage formula based on the tow duration (Theilacker 1980), and then converted to age (t days) using a two-cycle Gompertz growth curve. The first cycle is from hatching to yolk-sac absorption, a temperature-dependent growth curve, and the second cycle is from yolk-sac absorption to 22 mm larvae, a food-dependent growth curve (Zweifel and Hunter footnote 2; Methot and Hewitt footnote 3; Lo 1983). Larval abundance by length (age) group was estimated using a negative binomial weighted model (Bissell 1972; Zweifel and Smith 1981) which incorporates the "effective sampler size" (relative sampler bias). All larval abundance data were adjusted to conform to the following standard conditions: no extrusion, no day-night difference in avoidance, and a constant water volume filtered per unit depth. These data were converted to daily production (P_t) by dividing the total number of larvae in each length group by the duration (the number of days larvae remain within each length

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

group). It was necessary to compute a weighted mean of larval production ($_wP_t$) because the number of net tows was not proportional to the area size: The daily larval production (P_{t_j}, t_j) was estimated first for each of the three subareas (j = 1: inshore = regions 7 and 11; j = 2: nearshore = regions 4, 8, and 13; and j = 3: offshore = regions 5, 9, and 14) (Fig. 1). The data set ($_wP_t$, t) was used for final fitting of the mortality curve where $_wP_t = \sum_{j=1}^{3} P_{tj} u_j$, and u_j = 0.17, 0.31, and 0.52 for j = 1, 2, and 3, the relative area sizes. The unweighted average age $\bar{t}$ over three areas was used because little variation exists among t_j's (Fig. 2).

DAILY LARVAL PRODUCTION PER 0.05 m^2 ($_wP_t$) AT AGE t, 1979

PRESERVED SIZE (mm)	LIVE SIZE (mm)	(t) AVE AGE (day)	($_wP_t$) DAILY LARVAL PROD /0.05 m^2
2 50	3.26	4 91	0 518
3 75	4 57	8 60	0 121
4 75	5.69	11 58	0 0838
5.75	6.27	14 15	0 0665
6.75	7.83	16 41	0 0481
7 75	8 87	18 62	0 036

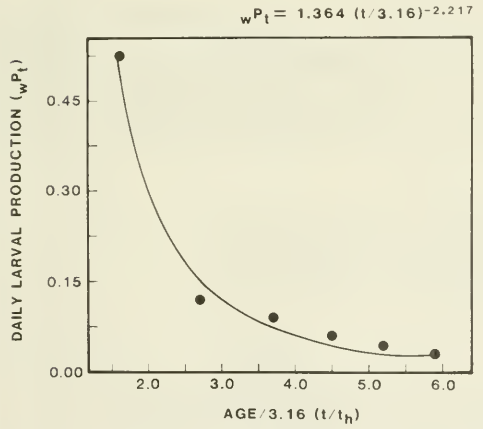

FIGURE 2.—Weighted daily larval production ($_wP_t$) and age in days (t) of northern anchovy and the fitted larval mortality curve based upon Equation (8B) for larvae < 20 d old, 1979.

MODEL

If a cohort of eggs (larvae) is followed and N_t is defined as the number of eggs (larvae) at age t (days), then the ratio N_t/N_0 measures the survival probability at age t: $S(t; z(t)) = P(T > t; z(t))$. The sample ratio n_t/n_0 estimates the survival probability $S(t)$ where $z(t)$, the instantaneous mortality rate (IMR), is defined as $\lim_{\Delta t \to 0} \frac{P(t < T < t + \Delta t \mid T > t)}{\Delta t}$. If the sample data (n_t, t) are taken from a single cohort and the form of $S(t)$ is known, both N_0 and $z(t)$ can be estimated through $n_t = n_0\, S((t); z(t))$. Assuming that the standing stock of eggs and larvae represents a single cohort (with stable age distribution) as it ages, then (N_t, t) can be estimated from the number of eggs and larvae in various stages (lengths) which are later converted to age in the sample. Hewitt (1982) conducted a simulation study to check for possible bias in larval mortality rate caused by seasonal changes in the intensity of spawning of northern anchovy which violates the assumption of a stable age distribution. He found that mortality was overestimated in the beginning (January-February) of a season when spawning was increasing and underestimated at the end (May-July) when spawning was decreasing. When the larval numbers were accumulated over the entire season, these two biases tended to cancel out. Therefore, the stable age distribution is a reasonable assumption if the egg and larval sample covers the entire season. To compute larval mortality for each year, I chose larval data from January to April to be consistent with the current sampling scheme. According to Hewitt's study, the larval mortality may be overestimated. However, because only young larvae (<8 mm preserved length) were considered in the model, the upward bias is slight. The number of eggs and larvae at various stages or length classes (n_{t_i}), as mentioned in a previous section, was further adjusted for the duration in days that eggs (larvae) remained in a particular stage or length class (d_i), i.e., $P_{t_i} = n_{t_i}/d_i$. The quantity P_{t_i} is egg (larval) production per day per unit area (e.g., 0.05 m^2) at age t_i, the average age of eggs (larvae) in the ith stage (length) class (Farris 1960; Saville 1964; Harding and Talbot 1973; Ciechomski and Capezzani 1973). (In later sections, the subscript i is dropped, thus (P_t, t) is used in place of (P_{t_i}, t_i).)

The model is based on the form of the mortality curves of northern anchovy eggs and those for anchovy larvae, the form of the curve for eggs and larvae being distinctly different. The daily egg and larval production P_t is modeled by three survivorship functions S_1, S_2, and S_3:

$$P_t = P_0 S(t) = \begin{cases} P_0\, S_1(t; z_1(t)) & t \leq t_c \quad (3A) \\ P_{t_c}\, S_2(t; z_2(t) \mid T > t_c) & t_c < t < 20\,\text{d} \quad (3B) \\ P_{t_k}\, S_3(t; z_3(t) \mid T > t_k) & t_k < t \quad (3C) \end{cases}$$

with the IMR

$$z(t) = \begin{cases} z_1(t) & t \le t_c \\ z_2(t) & t_c < t < 20 \text{ d} \\ z_3(t) & t_k < t \end{cases}$$

where $S_2(t; z(t) \mid T > t_c) = P(T > t; z(t) \mid T > t_c)$,
t_c is the age when the form of IMR changes,
t_k is max t_i for $t_i < 20$ d where t_i is the average age for the ith length class.

The quality of larval data for larvae older than 20 d is questionable because older larvae avoid the net (Hewitt 1982). The forms of $z_3(t)$ and $S_3(t)$ for $t > 20$ d are unknown at the present time. Therefore, only the mortality of eggs and larvae <20 d old was assessed.

The IMR, $z(t)$, relates to the survivorship function $S(t)$, by definition, in the form of

$$S(t) = e^{-\int_0^t z(u)du} = \begin{cases} e^{-\int_0^t z_1(u)du} = S_1(t) & t \le t_c \\ e^{-\int_0^{t_c} z_1(u)du - \int_{t_c}^t z_2(u)du} & t_c < t < 20 \\ = S_1(t_c)\, S_2(t \mid T > t_c) \\ = S_2(t). \end{cases} \quad (4)$$

The critical age t_c was defined as the age before which $z(t) = z_1(t)$, after which $z(t) = z_2(t)$. P_t and t from larval data were used to estimate both P_{t_c} and $z_2(t)$ through Equation (3B) after $S(t)$ is specified. Both larval production (P_{t_c}) and the standing stocks of eggs and larvae up to age t_c (m_{t_c}) were then used to estimate P_0 and $z_1(t)$ through Equation (3A) as below:

$$m_{t_c} = \int_0^{t_c} P_t\, dt = \int_0^{t_c} P_0\, S_1(t; z_1(t))\, dt \quad (5A)$$

and

$$P_{t_c} = P_0\, S_1(t_c; z_1(t)). \quad (5B)$$

Now I have two Equations (5A) and (5B) to be solved simultaneously for the unknowns P_0 and the parameters in $z_1(t)$. An iterative procedure was used to obtain estimates of P_0 and $z_1(t)$. Clearly, the selection of the function forms of $z_1(t)$ and $z_2(t)$ are important in obtaining accurate estimates of P_0 and P_{t_c}.

Anchovy Mortality Curves and Estimation of Egg Production

Daily egg and larval production per 0.05 m^2 and their ages (P_t, t) were estimated for 1979-81 to model the mortality curves $P_0\ S_1(t)$ and $P_{t_c}\ S_2(t \mid T > t_c)$ (Equation (3)). The egg data were collected in vertical net tows from 70 m with the

TABLE 1.—Daily egg and larval production per 0.05 m^2 (P_t) at various ages in days (t) sampled from CalVET and bongo tows, and the estimates of five parameters: egg production at age zero ($\hat{P}_0$), egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), larval production at hatching ($\hat{P}_I$) and incubation time in days (t_I) in CalCOFI regions 4, 7, 8, and 11, January-April 1979-81.

		1979[1]		Live standard length (mm)	1980		1981		Live standard length (mm)[2]	
		t	P_t		t	P_t	t	P_t		
Eggs	CalVET net	0.4167	10.79		0.4167	9.34	0.4167	5.64		
		0.9167	4.36		0.9167	9.22	0.9167	7.66		
		1.4167	4.91		1.4167	6.34	1.4167	4.87		
		1.9167	4.58		1.9167	4.71	1.9167	6.05		
		2.4167	6.87		2.4167	5.14	2.4167	4.84		
		2.9167	3.63							
Larvae	CalVET net	3.73	2.64	3.03	2.94	2.26	3.14	3.23	3.03	
					4.08	2.39	4.35	2.99	3.59	
					5.91	0.99	6.25	2.10	4.13	
					7.69	0.86	8.08	1.84	4.66	
	Bongo net	4.72	1.96	3.26	3.05	2.35	3.10	5.29	2.97	
		8.32	0.48	4.17	5.65	1.04	5.86	1.96	4.00	
		11.49	0.35	5.69	8.90	0.49	9.22	1.10	5.13	
		13.90	0.25	6.77	11.47	0.39	11.79	0.72	6.23	
		16.24	0.19	7.83	13.83	0.26	14.01	0.54	7.30	
		18.31	0.13	8.87	15.91	0.21	16.01	0.53	8.35	
					17.99	0.15	18.22	0.41	9.38	
$\hat{P}_0$			9.76	[3](2.82)	11.46	(1.27)	6.73	(1.32)		
$\hat{\alpha}$			0.33	(0.28)	0.38	(0.09)	0.11	(0.13)		
$\hat{\beta}$			1.83	(0.14)	1.24	(0.17)	1.19	(0.17)		
$\hat{P}_I$			3.59	(0.18)	2.51	(0.19)	4.81	(0.42)		
t_I			3.21		2.96		2.85			

[1]Not weighted by area size.
[2]For both 1980 and 1981 larval data.
[3]Asymptotic standard error in parentheses.

CalVET net, and the larval data were collected with both bongo oblique tows and the CalVET nets. The egg and larval catches by age group were standardized, that is, corrected for possible biases caused by extrusion through the mesh, day-night difference in avoiding the net, variation in the amount of water filtered, and the variation of larval growth rates which is both temperature and food dependent (Methot 1981; Lo 1983). The standardized daily egg and larval production estimates per 0.05 m^2 sea surface area in CalCOFI regions 4, 7, 8, and 11 for January-April 1979-81 are given (Table 1, Fig. 3).

The IMR for the egg stage was believed to be constant, $z_1(t) = \alpha$, (Stauffer and Picquelle footnote 6), whereas the IMR for larval stage was found to be age dependent $z_2(t) = \beta/t$ (a Pareto hazard function, Johnson and Kotz 1970). I first calculated sample IMR $z(t_i) = (P_{t_{i-1}} - P_{t_i})/(t_i - t_{i-1})/P_{t_i}$ which is an approximation of $dS(t)/dt/S(t)$ at various t for $0 < t < 20$ d using 1980 standardized egg and larval data listed in Table 1. The 1980 egg and larval production and age data were further combined so that $z(t) > 0$ for all t. The relationship between $z(t)$ and t determined the function form of $z(t)$ (Table 2). The $z(t)$'s were

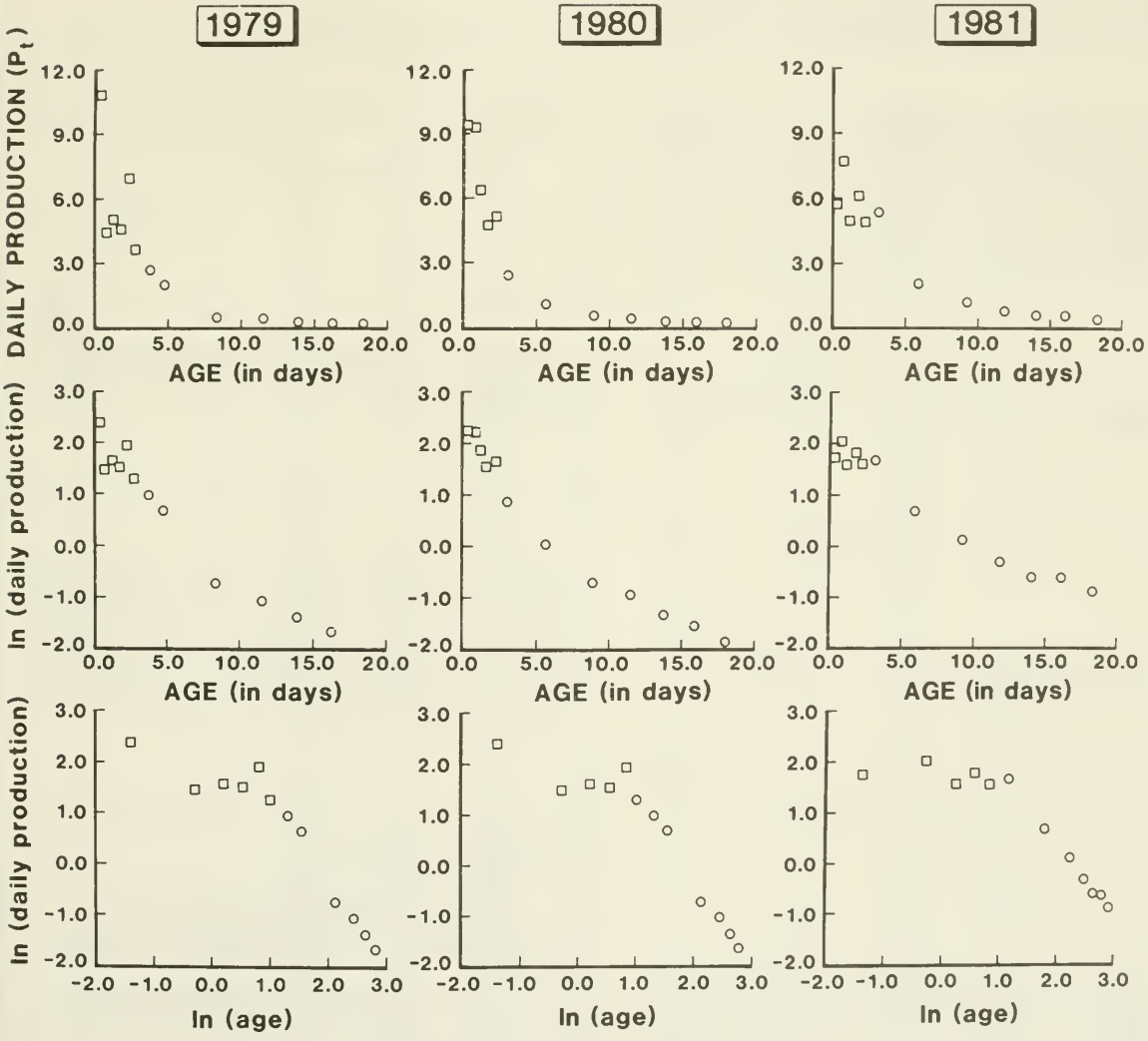

FIGURE 3.—Daily egg and larval production of northern anchovy per 0.05 m^2 (P_t) by age in days (t) and their log transformations ($\ln(P_t)$), 1979-81. A linear relationship between $\ln(P_t)$ and t indicates a constant instantaneous mortality rate (IMR) and a curvilinear relationship between $\ln(P_t)$ and t indicates an age dependent IMR. Squares are egg data and open circles are larval data.

TABLE 2.—The instantaneous mortality rates of anchovy eggs and larvae < 20 days ($z(t_i)$) by age in days ($\bar{t}_i$) computed from the daily egg and larval production estimates (P_{t_i}) and age (t_i), 1980. $z(t) = 0.0060 + 1.63/t$ is the function fitted to the data in the last two columns for $t > 4.5$ d.

i	t_i (d)	Daily egg and larval production P_{t_i}	$P_{t_{i-1}} - P_{t_i}$	$t_i - t_{i-1}$	$\bar{t}_i = (t_i + t_{i-1})/2$	$z(t_i)$[1]
1	0.67	9.28				
2	1.67	5.53	3.75	1.00	1.17	0.40
3	2.60	3.70	1.83	0.93	2.14	0.36
4	3.57	2.37	1.33	0.97	3.09	0.37
5	5.65	1.04	2.28	2.08	4.61	0.46
6	5.91	0.99	0.05	0.26	5.78	0.18
7	7.69	0.86	0.13	1.78	6.80	0.07
8	8.90	0.49	0.37	1.21	8.30	0.36
9	11.47	0.39	0.10	2.57	10.19	0.08
10	13.83	0.26	0.13	2.36	12.65	0.14
11	15.91	0.21	0.05	2.08	14.87	0.09
12	17.99	0.15	0.06	2.08	16.95	0.14

[1] $z(t_i) = (P_{t_{i-1}} - P_{t_i})/(t_i - t_{i-1})/P_{t_i}$.

quite constant for egg and larvae < 4.5 d old and decreased thereafter. For t values > 4.5 d, the function $z(t) = a + b/t$ fit the data best. Based upon the function relationship $z(t) = b/t$ (the intercept a is not distinguishable from zero and thus was dropped), I have the IMR $z(t)$:

$$z(t) = \begin{cases} \alpha & t \leq t_c \\ \beta/t & t_c < t < 20. \end{cases} \tag{6}$$

Applying Equation (6) to Equation (4) leads to

$$S(t) = \begin{cases} S_1(t) = e^{-\alpha t} & t \leq t_c \\ S_2(t) = e^{-\alpha t_c}\left(\frac{t}{t_c}\right)^{-\beta} & t_c < t < 20. \end{cases} \tag{7}$$

Combining Equations (3) and (7) one has

$$P_t = \begin{cases} P_0\, e^{-\alpha t} & t \leq t_c \\ P_0\, e^{-\alpha t_c}\left(\frac{t}{t_c}\right)^{-\beta} & t_c < t < 20 \end{cases} \tag{8A}$$

$$= P_{t_c}\left(\frac{t}{t_c}\right)^{-\beta}. \tag{8B}$$

To validate both Equations (8A) and (8B), logarithms of P_t and t were plotted: $\ln(P_t)$ against t should be a straight line for $t \leq t_c$ (Equation (8A)) and $\ln(P_t)$ against $\ln(t)$ should be a straight line for $t_c < t < 20$ (Equation (8B)) (Fig. 3). This was true for egg and larval production from 1979 to 1981. The determination of t_c, the age at which IMR changes, was subjective. Two values of t_c were used: One was the time of hatching or the duration of incubation (t_I) which is temperature dependent and the other was the average age of yolk-sac larvae (embryonic period) $t_c = t_{ys}$: $t_{2.5\,\mathrm{mm}}$ = age at preserved length 2.5 mm (about 5 d old). When t_c was considered equivalent to the incubation time ($t_c = t_I$), the egg stages were considered as one group with constant IMR; and when t_c was equivalent to average age of the yolk-sac larvae ($t_c = t_{ys}$), egg stages and yolk-sac length class(es) were considered as one group with constant IMR. In either case, P_{t_c} was estimated from the fitted curve

$$P_t = P_{t_I}\left(\frac{t}{t_I}\right)^{-\beta}, \text{i.e., } \hat{P}_{t_c} = \hat{P}_{t_I}\left(\frac{t_c}{t_I}\right)^{-\hat{\beta}}.$$

Substitution of Equation (7) in Equation (5) gives

$$m_{t_c} = \begin{cases} \int_0^{t_c} P_0\, e^{-\alpha t}\, dt = P_0(1 - e^{-\alpha t_c})/\alpha & \alpha > 0 \\ t_c \cdot P_0 & \alpha = 0 \end{cases} \tag{9A}$$

$$P_{t_c} = P_0\, e^{-\alpha t_c} \tag{9B}$$

where m_{t_c} is the standing stock of eggs and larvae up to age t_c. Equation (9A) divided by Equation (9B) results in

$$q = \begin{cases} m_{t_c}/P_{t_c} = (e^{\alpha t_c} - 1)/\alpha = \mathrm{h}(\alpha) & \alpha > 0 \\ t_c & \alpha = 0 \end{cases} \tag{10}$$

where $t_c = t_I$ or t_{ys} and q is the ratio of standing stock of eggs and larvae up to age t_c to the larval production P_{t_c}. The estimated IMR, $\hat{\alpha}$, was obtained by an iterative procedure using Equation (10). The estimated egg production obtained by rearranging the terms in Equation (9B):

$$\hat{P}_0 = \hat{P}_{t_c} \cdot e^{\hat{\alpha} t_c}.$$

The approximate variance of $\hat{\alpha}$ and $\hat{\beta}$ were computed in the appendix.

TIME SERIES ESTIMATES OF HISTORICAL EGG PRODUCTION (HEP)

The HEP per 0.05 m^2 (P_0) and the egg IMR (α) for the central stock of northern anchovy in the first 4 mo of the year, 1951-82, were estimated based upon Equations (9B) and (10). For years after 1978, catch data were available for CalVET and bongo nets, but I chose to use samples from

bongo nets because only bongo or similar nets (1 m ring nets) were used for sampling eggs and larvae prior to 1978.

Two series of HEP estimates were constructed. Series 1 assumed a constant IMR for the egg stage with $t_c = t_I$, whereas series 2 with $t_c = t_{ys}$ assumed a constant IMR throughout the embryonic period (Table 3). Both P_{tI} and P_{tys}, the daily larval production at hatching and yolk-sac stage, were obtained from the fitted line of Equation (8B) with $t_c = t_I$.

Under series 1, nearly half of the egg IMR ($\hat{\alpha}$) were negative (11 out of 24 yr). This was because the egg IMR depended on the value of q through Equation (10) where $q = m_{tI}/P_{tI}$. However, judging from Equation (10), $q = t_I$ for $\alpha = 0$. Therefore for those years where $q < t_I$, egg IMR would be less than 0. The small q's could result from the underestimated m_{tI} or overestimated P_{tI} or both. The poor results of IMR ($\hat{\alpha}$) were likely due to the underestimation of m_{tI}. As a result, the standing stock of eggs and that of yolk-sac larvae were combined into one group in series 2, to eliminate the negative IMR's.

TABLE 3.—Two time series of estimated historical egg production ($\hat{P}_0$), and egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), mean egg abundance (m_{tI}), mean egg and yolk-sac larval abundance (m_{tys}), January-April, and mean larval abundance (L_a) per 0.05 m^2, 1951-82 with standard error in parentheses.

	[1]Series 1		[1]Series 2					
Year	Daily egg production P_0	Egg mortality $\hat{\alpha}$	Daily egg production P_0	Egg mortality $\hat{\alpha}$	Larval mortality coeff. $\hat{\beta}$	Mean egg abundance m_{tI}	Mean yolk-sac larval abundance m_{tys}	Mean larval abundance[2] L_a
1951	0.006	0.03	0.012	0.23	0.85	0.02	0.03	0.04
	(0.024)	(1.34)	(0.116)	(2.18)	(0.15)	(0.03)	(0.03)	
1952	0.002	−0.57	0.017	0.09	0.88	0.02	0.07	0.04
	(0.003)	(0.35)	(0.107)	(1.27)	(0.20)	—	(0.01)	
1953	0.026	−0.08	0.066	0.19	0.95	0.11	0.21	0.011
	(0.019)	(0.20)	(0.180)	(0.54)	(0.10)	(0.03)	(0.03)	
1954	0.031	−0.48	0.168	0.12	1.16	0.24	0.61	0.17
	(0.026)	(0.26)	(0.188)	(0.24)	(0.07)	(0.08)	(0.08)	
1955	0.026	−0.77	0.316	0.07	1.01	0.39	1.27	0.19
	(0.028)	(0.32)	(0.393)	(0.26)	(0.17)	(0.12)	(0.14)	
1956	0.122	0.33	0.146	0.33	0.88	0.25	0.36	0.11
	(0.114)	(0.26)	(0.647)	(0.88)	(0.24)	(0.12)	(0.12)	
1957	0.148	−0.12	0.364	0.20	0.94	0.54	1.09	0.26
	(0.040)	(0.31)	(0.423)	(0.25)	(0.10)	(0.23)	(0.24)	
1958	0.966	0.40	1.274	0.43	0.88	1.61	2.44	0.33
	(0.481)	(0.18)	(1.182)	(0.23)	(0.08)	(0.45)	(0.93)	
1959	0.444	−0.11	0.992	0.23	1.18	1.47	2.68	0.34
	(0.267)	(0.21)	(0.822)	(0.20)	(0.16)	(0.36)	(0.38)	
1960	0.678	−0.18	1.765	0.24	1.80	2.78	4.85	0.34
	(0.535)	(0.26)	(0.774)	(0.10)	(0.06)	(0.99)	(0.99)	
1961	0.446	0.25	0.653	0.29	1.55	0.94	1.59	0.26
	(0.669)	(0.43)	(0.635)	(0.22)	(0.16)	(0.28)	(0.28)	
1962	0.443	−0.18	1.314	0.19	1.08	2.09	4.15	0.67
	(0.297)	(0.18)	(1.171)	(0.18)	(0.23)	(0.50)	(0.58)	
1963	1.404	0.16	2.275	0.28	0.81	3.57	5.92	0.95
	(0.690)	(0.15)	(0.991)	(0.09)	(0.04)	(0.93)	(0.93)	
1964	3.681	0.43	4.147	0.42	1.44	6.39	8.55	0.65
	(1.956)	(0.15)	(2.681)	(0.13)	(0.21)	(1.80)	(1.81)	
1965	0.778	−0.45	4.019	0.19	2.42	6.48	12.78	1.04
	(0.559)	(0.21)	(1.176)	(0.06)	(0.12)	(1.75)	(1.75)	
1966	3.540	0.26	5.256	0.42	1.84	7.82	10.61	0.80
	(1.660)	(0.14)	(1.799)	(0.07)	(0.04)	(2.11)	(2.11)	
1969	0.876	−0.42	3.821	0.19	2.15	6.16	12.14	0.67
	(0.557)	(0.19)	(1.062)	(0.06)	(0.08)	(1.53)	(1.53)	
1972	0.639	−0.09	1.657	0.25	1.73	2.56	4.52	0.62
	(0.356)	(0.16)	(0.804)	(0.11)	(0.11)	(0.66)	(0.67)	
1975	15.320	0.36	19.691	0.44	1.88	30.06	39.14	0.81
	(11.608)	(0.22)	(10.364)	(0.11)	(0.20)	(4.40)	(14.41)	
1978	10.524	0.64	10.738	0.59	1.66	13.58	16.60	0.29
	(4.566)	(0.15)	(4.484)	(0.10)	(0.10)	(3.67)	(3.67)	
1979	4.258	0.36	5.426	0.48	2.22	8.06	10.05	0.39
	(2.215)	(0.16)	(2.616)	(0.10)	(0.15)	(2.39)	(2.39)	
1980	2.338	0.37	2.671	0.36	1.22	4.12	6.48	0.40
	(1.427)	(0.22)	(1.260)	(0.08)	(0.03)	(1.46)	(1.46)	
1981	3.95	0.36	4.376	0.38	1.53	6.88	10.29	0.63
	(2.658)	(0.24)	(2.084)	(0.08)	(0.03)	(2.70)	(2.70)	
1982	1.941	0.15	3.294	0.36	1.81	4.93	7.33	0.46
	(1.230)	(0.20)	(1.367)	(0.09)	(0.04)	(1.70)	(1.70)	

[1]Series 1 and 2 are two methods used for estimating daily egg production (P_0). Series 1 assumed a constant IMR for egg stage whereas series 2 assumed a constant IMR for egg through yolk-sac larval stage.
[2]Computed from annual larval abundance for the central subpopulation (Table 2, Stauffer and Charter 1982).

Under series 2, P_0 and α were estimated based upon $q = m_{t_{ys}}/P_{t_{ys}}$ (Equations (9B) and (10)), with $t_c = t_{ys}$. The average age of yolk-sac larvae ($t_{ys} = t_{2.5\ mm}$) was 4.7 d. All q's were greater than t_{ys}, thus $\hat{\alpha}$'s were all positive.

The HEP (P_0) for both series have the same trend: a gradual increase from the early 1950's to middle 1960's, thereafter fluctuating until 1975 when it reached the peak value at 15.32/day per 0.05 m^2 (series 1) or 19.69/day per 0.05 m^2 (series 2). From 1978, HEP decreased to the present level of 1.94/day per 0.05 m^2 (series 1) and 3.29/day per 0.05 m^2 (series 2) (Table 3, Fig. 4). The approximate standard error of the estimated HEP (P_0) and egg mortality ($\hat{\alpha}$) is large for the early years and small for the recent years, possibly because of the poor quality of early egg data, or an insufficiency of the delta method to estimate the variance.

For the purpose of verification, HEP (P_0) from the two series based upon the egg-larval mortality model and the egg production at age 0 estimated from the current EPM (Stauffer and Picquelle footnote 6) were compared for 1980-82 where adequate egg and larval samples were available (Table 4). The P_0's from the two series of HEP and the current EPM were not significantly different, nor were the egg mortality rates. However, the point estimates of P_0's from the current EPM were lower than those estimated from the two series. The reason for the lower values is unknown at the moment. This could be due to random fluctuation of the statistics. The current EPM estimates of P_0 were much more precise than those derived from the historical egg-larval mortality model, whereas the precision of egg mortality rate from both methods was similar.

As to the estimates from the two series of HEP, the point estimates of P_0 from series 2 were always higher than those estimated from series 1. Recall that the assumption of series 2 was that the egg through yolk-sac larval stage suffers a constant mortality rate. However, if in fact the yolk-sac larvae suffer a higher mortality rate than eggs, the mortality rate of eggs and larvae when combined (series 2) would overestimate egg mortality as well as egg production (P_0) (Equation (9B)).

TABLE 4.—Daily egg production per 0.05 m^2 ($\hat{P}_0$), egg instantaneous mortality ($\hat{\alpha}$), egg abundance (m_{tl}) of northern anchovy, and number of tows (n) in CalCOFI regions 4, 5, 7, 8, 9, 11, 13, and 14, January-April 1980-82.

	1980		1981		1982	
	$\hat{P}_0$ (SE)	$\hat{\alpha}$ (SE)	$\hat{P}_0$ (SE)	$\hat{\alpha}$ (SE)	$\hat{P}_0$ (SE)	$\hat{\alpha}$ (SE)
Historical egg production						
Series 1	2.33	0.37	3.95	0.36	1.94	0.15
	(1.46)	(0.21)	(2.70)	(0.24)	(1.70)	(0.20)
Series 2	2.67	0.36	4.37	0.38	3.29	0.36
	(1.46)	(0.08)	(2.70)	(0.08)	(1.70)	(0.09)
Current egg production method[1]	2.29	0.45	1.82	0.14	1.18	0.15
	(0.51)	(0.11)	(0.31)	(0.08)	(0.32)	(0.104)

	1980		1981		1982	
Egg abundance per 0.05 m^2 (m_{tl})	n	m_{tl} (SE)	n	m_{tl} (SE)	n	m_{tl} (SE)
CalVET (0.333 mm)[2]	961	3.20	1,134	4.72	992	3.48
		(0.52)		(0.72)		(0.62)
Bongo (0.505 mm)	97	4.12	403	6.88	113	4.93
		(1.46)		(2.70)		(1.70)

[1] Picquelle, see text footnote 8.
[2] Mesh size.

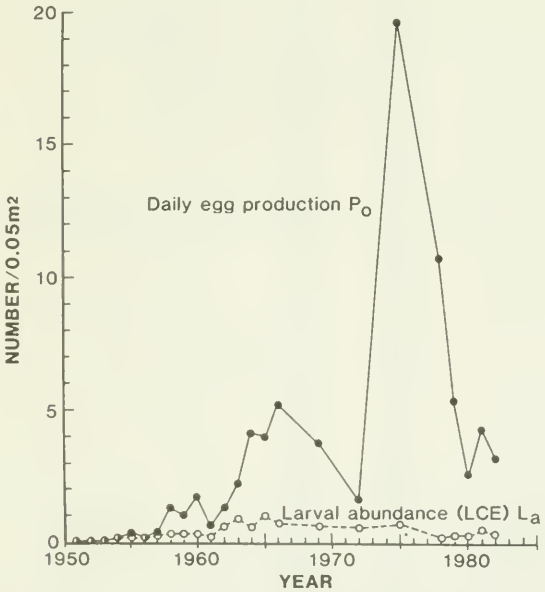

FIGURE 4.—Estimates of historical egg production of the central stock of northern anchovy using the series 2 method (P_0) and the larval abundance (L_a) of the larval census estimates, 1951-82.

DISCUSSION

Historical production (P_0) and egg IMR (α) of the central stock of northern anchovy for the first 4 mo of the year from 1951 to 1982 were estimated based upon the information of total number of eggs and yolk-sac larvae per 0.05 m^2 and the egg-larval mortality model. Two series of P_0 and α were produced. Series 1 assumed a constant IMR for only the egg stage whereas series 2 assumed a constant IMR for the entire embryonic period. Both series of P_0 showed the same trend (Table 3, Fig. 4) with a peak in 1975. The high daily egg

production estimate (P_0) in 1975 was caused by the high standing stock of eggs (m_{tI} = 30.06/0.05 m^3 per m depth) which was more than 10 times that of other years, and the high egg IMR ($\hat{\alpha}$ = 0.36) (Table 3). The high daily egg production in 1975 reflects either a high fecundity (high spawning frequency) or a high spawning biomass or some combination of these effects. The present level of egg production is the same as that in the middle 1960's. Both egg IMR ($\hat{\alpha}$) and larval IMR coefficient $\hat{\beta}$, $z(t) = \beta/t$, vary from year to year (Fig. 5).

In addition to providing a 24-yr time series of HEP for the northern anchovy, two important conclusions can be drawn from this analysis:

1. The form of IMR of eggs (and yolk-sac larvae) is different from that of older larvae (6-20 d).
2. Egg production is a better index of stock abundance than is the standing stock of larvae.

Little doubt exists that mortality rates change sometime between the hatching of the eggs and the onset of feeding. Analysis of the daily egg and larval production by age for 1979-81 (Fig. 3) suggested a constant IMR for eggs (or eggs and yolk-sac larvae) and an age-dependent IMR of Pareto form for older larvae ($z(t) = \beta/t$ for $t_c < t <$ 20 d) (Table 2). The age t_c in Equation (3) could be considered to mark the end of the critical period after which mortality decreases (Ahlstrom 1954; Marr 1956; Farris 1960; Saville 1964). Series 1 assumed t_c = incubation time and series 2 assumed t_c = average age of yolk-sac larvae. From the existing data, I could not ascertain which assumption was the more likely, but it was evident that larvae at hatching or near first-feeding (yolk absorption) suffer higher mortality than do older larvae.

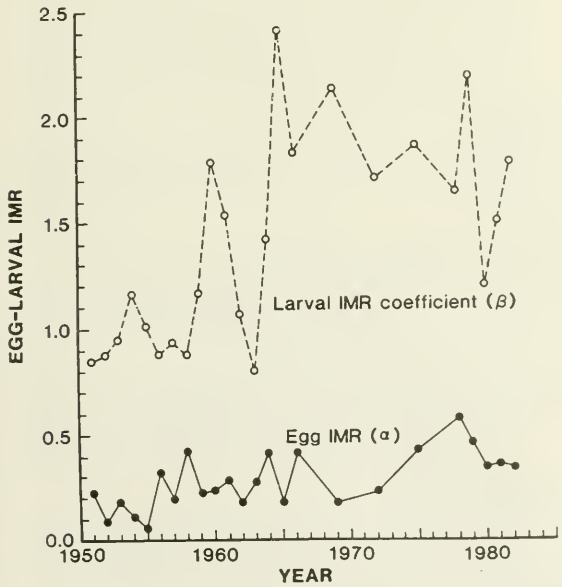

FIGURE 5.—Estimated egg instantaneous mortality rate (IMR) ($\hat{\alpha}$) from series 2 method of estimating egg production and the larval mortality coefficient ($\hat{\beta}$) of the central stock of northern anchovy, 1951-82.

The HEP (P_0) is certainly preferable to larval standing stock (larval census estimate = LCE) for use as an index of spawning biomass. Egg production is related to the spawning biomass through Equation (2), i.e., $P_0 = B_a \cdot C$, where the proportionality C is the reproductive output ($R \cdot F \cdot E/W$). If the reproductive output remains constant between years, as shown by 1980-82 anchovy data (Picquelle[8]), the HEP will be an unbiased index of the spawning biomass. The LEC assumes $B_a = K \cdot L_a$ where L_a is the larval abundance and K is a constant proportionality (Smith 1972; Stauffer and Charter 1982) (Table 3, Fig. 4). Thus to provide an unbiased index of biomass, the method requires that not only the reproductive output be constant from year to year but also the egg and larval mortality must remain constant as well. Using Equation (8), the larval abundance (age < 30 d old) can be written as

$$L_a = \int_{t_I}^{30} P_t \, dt$$

$$= \int_{t_I}^{30} P_0 \, S(t; z(t)) \, dt$$

$$= B_a \left(\frac{R \cdot F \cdot E}{W}\right) g(\alpha, \beta, t_I)$$

where $g(\alpha, \beta, t_I) = \begin{cases} e^{-\alpha t_I} \dfrac{t_I}{\beta - 1}\left[1 - \left(\dfrac{30}{t_I}\right)^{-(\beta-1)}\right] & \text{for } \beta \neq 1 \\ e^{-\alpha t_I}(\ln 30 - \ln t_I) & \beta = 1 \end{cases}$

α is the egg IMR and β is the larval mortality coefficient.

The larval abundance (L_a) is proportional to the spawning biomass (B_a) with constant proportionality only if the reproductive output

[8]S. J. Picquelle, Statistician, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E, Seattle, WA 98112, pers. commun. July 1983.

($R \cdot F \cdot E/W$) and the egg and larval mortality rates through the function g (α, β, t_1) remain constant from year to year. It is clear that from 1951 to 1982 time series (Table 3) that the assumption of constant egg and larval mortality has not been met by the central California anchovy population. The HEP requires constant reproductive output. The validity of this assumption can only be tested with future data.

In addition to the ichthyoplankton data, several other indices of anchovy biomass exist: acoustic trawl surveys conducted by California Department of Fish and Game, aerial survey records from aircraft associated with the fishery, catch-effort analysis (CPUE), and cohort analysis from the catch of the United States and Mexican fishery. In a recent management plan, all of these indices except cohort analysis have been calculated and compared with the time series of egg production presented in this paper (MacCall et al.[9]). The estimates of egg production covaried with these other indices from year to year and appeared to be the most consistent index of spawning biomass among these indices (Table 5).

Selection of the appropriate method for estimating biomass depends upon the data availability and knowledge of the growth of eggs and larvae. If nothing is known of the age of eggs and larvae and no information exists on reproductive parameters, the LCE is the only method available although subject to major biases. If egg and larval age data exist but no data on reproductive parameters are available, then the HEP is the preferable method. The EPM is the best method; it requires not only knowledge of egg mortality but accurate estimates of adult reproductive parameters as well. In many time series, both growth and abundance of eggs and larvae are available but reproductive parameters are not. In these cases, the HEP is probably the most accurate means of creating a historic time series of biomass.

[9]MacCall, A. D., R. D. Methot, D. D. Huppert, H. W. Frey, and O. Mathisen. 1983. Northern anchovy second draft revised fishery management plan incorporating DEIS/RIR. Pac. Fish. Manage. Counc.

TABLE 5.—Correlations among various indices of anchovy spawning biomass. Upper value is correlation coefficient, lower value is number of observations. (Reproduced from table 4.3-2 of MacCall et al. (text footnote 9).)

Historical egg production					
0.458	Larval				
(23)	census				
0.807	0.708	Acoustic			
(8)	(7)	survey			
0.818	0.327	0.659	Aerial		
(9)	(9)	(9)	index		
0.791	0.004	0.512	0.379	Spring	
(4)	(4)	(10)	(9)	CPUE	
0.395	0.865	0.290	0.655	0.256	Fall
(4)	(4)	(10)	(10)	(9)	CPUE

Spawning biomass index	Consistency[1]	Rank
Historical egg production	0.654	1
Larval census	0.480	5
Acoustic survey	0.606	2
Aerial index	0.583	3
Spring CPUE	0.388	6
Fall CPUE	0.517	4

[1]Consistency is average of correlation coefficients.

ACKNOWLEDGMENTS

I thank John Hunter, Roger Hewitt, Paul Smith, Rick Methot, Alec MacCall, Jay Barlow, National Marine Fisheries Service; David Farris, San Diego State University; Grace Yang, University of Maryland; two referees for reviewing the manuscript and making valuable suggestions. I also thank Barry Finzel, Cynthia Meyer, Carol Miller, and Richard Charter for compiling historical egg and larval data files, and Mary DeWitt and Debra Brown for typing the manuscript.

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APPENDIX

The approximate variances of $\hat{\alpha}$ and $\hat{P}_0$ were derived from the delta method (Seber 1973):

$$\operatorname{var}[f(x_1,\ldots,x_I)] \doteq \sum_{i=1}^{I}\left[\frac{\partial}{\partial x_i} f(x_1,\ldots,x_I)\right]^2 \operatorname{var}(x_i) + 2\sum_{i<j} \frac{\partial}{\partial x_i} f(x_1,\ldots,x_I)\,\frac{\partial}{\partial x_j} f(x_1,\ldots,x_I)\operatorname{cov}(x_i,x_j)\Bigg|_{\hat{E}x_i,\, i=1,\ldots,I}$$

var ($\hat{\alpha}$) was computed based upon Equation (10), i.e.,

$$\operatorname{var}(q) \doteq \left(\frac{\partial h(\alpha)}{\partial \alpha}\right)^2 \operatorname{var}(\hat{\alpha}).$$

Thus $\text{var}(\hat{\alpha}) \doteq \text{var}(q) \cdot \left(\frac{\partial h(\alpha)}{\partial \alpha}\right)^{-2}$

$$\doteq \text{var}(\hat{m}_{t_c}/\hat{P}_{t_c}) \left(\frac{\partial h(\alpha)}{\partial \alpha}\right)^{-2}$$

$$= \frac{\text{var}(\hat{m}_{t_c}) + q^2 \,\text{var}(\hat{P}_{t_c}) - 2q \,\text{cov}(\hat{m}_{t_c}, \hat{P}_{t_c})}{\hat{P}_{t_c}^{\,2}} \cdot \left[\hat{\alpha}^4 / \left\{e^{\hat{\alpha} t_c}(\hat{\alpha} t_c - 1) + 1\right\}^2\right]$$

where cov (m_{t_c}, P_{t_c}) was estimated from the 1951-82 time series. Var (P_0) was computed based upon Equation (9B)

$$\hat{P}_0 = \hat{P}_{t_c} e^{\hat{\alpha} t_c}$$

$$\text{var}(\hat{P}_0) \doteq \left\{\frac{\partial P_0}{\partial \alpha}\right\}^2 \text{var}(\hat{\alpha}) + \left\{\frac{\partial P_0}{\partial P_{t_c}}\right\}^2 \text{var}(\hat{P}_{t_c}) + 2\left(\frac{\partial P_0}{\partial \alpha}\right)\left(\frac{\partial P_0}{\partial P_{t_c}}\right) \text{cov}(\hat{P}_{t_c}, \hat{\alpha})\Big|_{\hat{\alpha},\, \hat{P}_{t_c}}$$

$$= e^{2\hat{\alpha} t_c}\left[t_c^{\,2}\, \hat{P}_{t_c}^{\,2}\, \text{var}(\hat{\alpha}) + \text{var}(\hat{P}_{t_c}) + 2\hat{P}_{t_c} \cdot t_c \cdot \text{cov}(\hat{P}_{t_c}, \hat{\alpha})\right]$$

where cov $(\hat{P}_{t_c}, \hat{\alpha})$ was estimated from the 1951-82 time series.

VERTICAL STRUCTURE OF NEARSHORE PLANKTON OFF SOUTHERN CALIFORNIA: A STORM AND A LARVAL FISH FOOD WEB

M. M. Mullin, E. R. Brooks, F. M. H. Reid,
J. Napp, and E. F. Stewart[1]

ABSTRACT

Samples of zooplankton and phytoplankton were taken at 5 m depth intervals in the upper 50 m of water off Dana Point, California, in the spring of 1980, just before and just after a local storm. Most of the 43 zooplanktonic taxa, many phytoplanktonic taxa, and chlorophyll were vertically stratified. After the storm, naupliar copepods, chlorophyll, and a few phytoplanktonic taxa were more abundant, and several zooplanktonic taxa were more concentrated in the upper layers. The storm did not decrease the vertical stratification of larval fish food, so the feeding environment after the storm was at least as favorable as that before the storm, but larval fish were less abundant.

Studies in the laboratory have provided data on the kinds and abundances of food which are required for survival and growth of some types of zooplankton found in the surface waters of the Southern California Bight (e.g., Mullin and Brooks 1970; Paffenhöfer 1976) and of the larvae of the anchovy, *Engraulis mordax*, (e.g., Hunter 1976; Lasker et al. 1970) and jack mackerel, *Trachurus symmetricus*, (Devonald 1983). The anchovy has overwhelmingly dominated the larval fish assemblage of the area in recent years (e.g., Gruber et al. 1982). Direct experimentation (Lasker 1975) and indirect comparison of metabolic requirements and observed concentrations of likely food (Mullin and Brooks 1976; Cox et al. 1983) have shown examples of situations where only in layers or patches of anomalously high concentration of food can larval fish or copepods obtain enough nutrition to grow. Field data on vertical distributions indicate that extensive, sharply defined layers with elevated abundances of phytoplankton often exist within the euphotic zone (e.g., Cullen and Eppley 1981, for chlorophyll; Kiefer and Lasker 1975, for *Gymnodinium splendens*; Cullen et al. 1982, for several species).

There is also more indirect evidence of the importance of unusually rich layers of food for the survival and growth of planktonic predators: The greater size of "wild" copepods relative to those raised in the laboratory (Mullin and Brooks 1970), the limitation of egg production of a copepod population (Checkley 1980b), and the failure of year classes of anchovy when storms or upwelling were thought to disrupt layers of food (Lasker 1981). However, direct field evidence concerning starvation or growth limitation by food of larval anchovy is both limited and contradictory (Arthur 1976; Methot and Kramer 1979; O'Connell 1980).

The population of the large copepod, *Calanus pacificus*, is sometimes concentrated in those layers where autotrophic phytoplankton is most abundant (Mullin and Brooks 1972, 1976). However, there also are cases where no such correlations were found (Mullin and Brooks[2]) or where *Calanus* and other herbivores actively avoided a layer of abundant dinoflagellates (Fiedler 1982), and where feeding in such a layer was depressed relative to other parts of the water column (Fiedler 1982; Huntley 1982). In the present study, we examined the vertical relations between several zooplanktonic taxa and chlorophyll, a measure of the autotrophic, phytoplanktonic biomass. Since the nutrition of zooplankton governs growth and fecundity, the vertical relations between zooplankters and their food can affect the future supply of food for fish if the zooplankton is food-limited.

Small-bodied species of zooplankton (or larval stages of larger species), some large-celled, nonthecate dinoflagellates, and protozoans were of particular interest as representing potential lar-

[1]Institute of Marine Resources, A-018, Scripps Institution of Oceanography, University of California—San Diego, La Jolla, CA 92093.

[2]Mullin, M. M., and E. R. Brooks. 1976. Unpubl. data. Institute of Marine Resources, Scripps Institution of Oceanography, University of California—San Diego, La Jolla, CA 92093.

Manuscript accepted May 1984.
FISHERY BULLETIN: VOL. 83, NO. 2, 1985.

val fish food. Larger zooplankters represent potential competitors with larval fish for dinoflagellate and protozoan prey, or even potential predators of the larvae themselves.

The vertical distribution of larval anchovy within the euphotic zone is less well known than is that of zooplankton, particularly with respect to the vertical distribution of their food sampled concurrently, because larval fish are so rare that nets with large capacity must be used to capture significant numbers of them. It was partly to provide such data that we conducted the present study concurrently with sampling by National Marine Fisheries Service personnel from a second vessel to determine the vertical distribution of larval fish. Records of water temperature, concentration of chlorophyll, and abundances of phytoplankton at the depth of the chlorophyll maximum were also taken from the second vessel, and are compared with our results below.

We were fortunate, intellectually if not physically, to sample a fixed location before and after passage of a local storm (cf. Lasker 1975), and we therefore tried to examine the potential importance for the food web of turbulent rearrangement of vertical distributions. We looked for changes coincident with the storm in overall abundances and in the intensity and patterns of vertical stratification of many planktonic taxa, and in correlations between the vertical distributions of predators and their potential prey. We then made predictions concerning the implications of these changes for the nutrition of larval fish.

METHODS

From mid-March to mid-April 1980, spawning of anchovy was concentrated in the inner portions of the Southern California Bight, apparently confined by plumes of cool water extending south of Point Conception beyond Santa Catalina and San Clemente Islands (Lasker et al. 1981). Between 29 March and 6 April, we took 13 vertical series of samples at 5 m intervals in the upper 50 m of water at lat. 33°28.5′N, long. 117°46.7′W (CalCOFI station 90.28, 3.5 km offshore from Dana Point, California), where the depth of water was ~350 m, using the pump and hose described by Mullin and Brooks (1976) and Mullin (1979). Almost all of the larval anchovy at this station occurred in the upper 40 m (Pommeranz[3]). Because of the restricted area of the anchovy's spawning at the time, our results may be indicative of conditions experienced by a considerable fraction of the larvae produced in late March-early April in the Bight. The volume of water filtered per quantitative sample of zooplankton was typically 200-300 l; for comparison, the rate at which a 1.5 cm larval anchovy searches water for food is about 5 l/h (Hunter 1972). In addition to quantitative, net-concentrated samples of zooplankton and fiberglass-filter concentrated samples of chlorophyll, we preserved unconcentrated samples of water in 5% v:v Formalin[4] for counts of phytoplankton, and filtered nonquantitative samples of net-caught zooplankters onto fiberglass filters which were then frozen for later analysis of plant pigments in the guts.

One profile was completed during 0900-1400 h and another during 2030-0030 h each 24-h day except from 0000 on 1 April to 0900 on 3 April, when a local storm kept us in port. Profiles 1-6 were "prestorm", 7-13 "poststorm".

Analytical procedures for chlorophyll and net-caught zooplankton followed Mullin and Brooks (1976) and Mullin (1979). All recognizable zooplankters were enumerated. For phytoplankton and protozoans, we prepared a physically integrated sample for each profile by mixing 50 ml of water taken from each of the 11 depths. Fifty ml of this integrated sample were settled for 48 h, and cells were counted using the Utermöhl method. For cells ~20 μm or greater (equivalent spherical diameter), half the settled material was counted at 160× magnification (equivalent to a 25 ml sample); for cells <20 μm, one row across the diameter of the settling chamber was studied at 625× magnification (0.33 ml).

Subsequently, 50 ml aliquots from each depth for each profile were settled at least 24 h and examined. Since the flora was very diverse, we selected a short list of taxa using the following criteria: Cells were clearly identifiable even after preservation in Formalin, present in sufficient numbers to provide reliable data, and (with several exceptions) of interest as possible larval fish food. We believe that all taxa usable as food were satisfactorily preserved and counted. Most of the cells were counted using 160× magnification, usually in an equivalent of a 12.5, 25, or 50 ml sample. *Chaetoceros* spp., *Nitzschia* spp., and *Emiliania* (*Coccolithus*) *huxleyi* were enumerated

[3]Tilman Pommeranz, Institut fur Meereskunde, Kiel, West Germany, pers. commun. 1984.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

at 250×, usually in one or two rows across the settling chamber (1.13 or 2.3 ml). A precipitate developed in certain samples after several months storage, so profiles 1, 2, 8, and 12 could not be included in the analysis based on discrete depths; profile 13 was also excluded in order to balance the data.

To measure the amount of plant pigments in the guts of selected zooplanktonic taxa, we used an approach similar to that of Mackas and Bohrer (1976). In a darkened room, the frozen contents of each fiberglass filter were washed onto a circle of Nitex mesh (180 μm) and then sucked dry. The mesh disk was transferred to a Petri dish, wetted, and then examined visually using low magnification and low-intensity green light. Organisms were removed singly from each mesh, dipped in filtered seawater, and then sorted into scintillation vials sitting in an ice bath and containing small amounts of 90% reagent grade acetone.

After obtaining enough organisms, we inspected the contents of each vial visually to insure that they were taxonomically homogeneous and to record the number of individuals present. The contents were then homogenized with a motor-driven teflon pestle in a glass grinding vessel to which $MgCO_3$ and acetone were added. The homogenate was transferred by several rinses to a 15 ml screw-cap test tube and the volume was adjusted to 10 ml. All test tubes were stored in a light-tight container in a refrigerator for ~1 h, after which the homogenates were given an additional half hour to extract and to warm to room temperature.

The homogenate from each tube was first mixed and then filtered through a fiberglass filter to remove the $MgCO_3$ and animal tissue/exoskeleton. The amounts of chlorophyll a and phaeopigments in the filtrate were determined fluorometrically (Holm-Hansen et al. 1965) using a Turner Model 111 fluorometer equipped with a high-sensitivity door.

In order to evaluate the method, we collected copepods by oblique net hauls over the Scripps Canyon (~2 km from shore), sorted them, and placed them in filtered seawater to starve for 18-24 h. On other occasions copepods were similarly collected, starved to void their guts, and then allowed to become satiated on mixtures of cultured phytoplankton. All animals were frozen before pigment extraction.

To assess (ex post facto) whether preservation of pigments by freezing was complete, we took oblique net tows (total duration ~2 h) over Scripps Canyon. Each net haul was immediately strained through pieces of Nitex (<100 μm) netting and then quick-frozen using dry ice. Twelve samples thus obtained were stored in the same freezer as the cruise samples and processed in a similar manner. One sample (T_0) was processed the same day, the other samples at various times thereafter up to 700 d. We were unable to detect a decrease in total pigments over this time period by linear regression, and therefore believe the freezing to be adequate.

The first group of hypotheses we wished to test concerned temporal changes in patterns of vertical distribution. One general procedure was to treat several samples of one kind (e.g., all diurnal samples from a particular depth before the storm) as replicates accounting for variability due to technique and to real patchiness, and then to look for significant differences through an analysis of variance (ANOVA) on log-transformed abundances. Details are in Table 1. This was done for those taxa for which the variances (of log-transformed data) were homogeneous by Bartlett's and/or Cochran's tests (Dixon and Massey 1957). Where the variances were heterogeneous (i.e., $P < 0.01$ of homogeneity), we tested analogous hypotheses through nonparametric tests, as indicated in Table 2. Taxa for which it was necessary to employ the battery of nonparametric tests are indicated by asterisks in the Appendix.

A second group of hypotheses concerned correlations between measured properties, such as the concentration of chlorophyll and the abundance of a particular taxon. These hypotheses were tested by nonparametric correlation or concordance tests; details are in Section C below. We also tested for changes in overall community composition by constructing dendrograms based on rank difference correlation coefficients. All nonparametric tests are from Tate and Clelland (1957).

RESULTS

The overall abundances and vertical distributions of 43 zooplanktonic and 18 phytoplanktonic and protozoan taxa in the upper 50 m are shown in the Appendix, based on median abundances for diurnal and nocturnal profiles, before and after the storm, together with the distributions of chlorophyll. Depending on dietary preferences of the visually feeding larval anchovy (e.g., Arthur 1976), some combination of the diurnal distributions of several taxa represents the "typical" vertical distribution of larval fish food (see Section D below). We will discuss results in the following

TABLE 1.—Three-way analysis of variance on log-transformed abundances (m^{-3}) (see Appendix). To balance the sampling design, the 13th profile for zooplankton and chlorophyll (6 April) was omitted from the analysis. A significance level of $P < 0.01$ was used to compensate for multiple testing of the same hypotheses for many taxa.

Classification of sample	Significance of ANOVA probably indicates:
1. Day vs. night	Taxon migrated dielly from below 50 m into sampled range. Diel variation in avoidance of hose intake would create spurious significance. For very short-lived taxa, strong diel variation in birth, death, or maturation could also cause significant differences.
2. Before vs. after storm	Taxon changed in mean abundance coincident with storm. Cannot distinguish advective from biological causes.
3. Depth	Taxon was nonuniformly distributed 0-50 m in a consistent manner (or avoidance varied with depth).
Interaction 1 × 2	Taxon migrated dielly into sampled range from below 50 m before or after storm, but not both.
Interaction 1 × 3	Taxon had some kind of diel migration. If classification 1 was not significant, migration occurred within upper 50 m. Variation in avoidance both dielly and with depth could create spurious significance.
Interaction 2 × 3	Depth distribution of taxon changed coincident with storm. Change could either result in greater or lesser uniformity with depth or a change in depth of the maximum.
Interaction 1 × 2 × 3	Pattern of diel migration of taxon changed coincident with storm.

TABLE 2.—Questions, hypotheses, and nonparametric statistical tests for taxa with heterogeneous variances (designated by asterisks in Appendix). A significance level of $P < 0.01$ was used to compensate for multiple testing.

Question	Null hypothesis (H_0)	Test and comments
1. What taxa migrated dielly from below 50 m into the sampled range?	No difference in abundance (m^{-2}), day vs. night.	Mann-Whitney U test for difference in median abundances (m^{-2}) of each taxon, day vs. night. Compare to ANOVA classification 1.
2. What taxa migrated dielly within the upper 50 m?	No difference in depth of median animal, day vs. night.	For each taxon for which H_0 1 is accepted, Mann-Whitney U test for difference in depth of median animal, day vs. night. Compare to ANOVA interaction 1 × 3.
3. What taxa changed in abundance coincident with the storm?	No difference in abundance (m^{-2}) before vs. after storm.	For each taxon for which H_0 1 is accepted, Mann-Whitney U test for difference in median abundances (m^{-2}), 29 March-1 April profiles vs. 3-6 April profiles. Compare to ANOVA classification 2.
4 What taxa became more or less uniform in vertical distribution following the storm?	No difference in range of abundances (m^{-3}) 0-50 m.	For each taxon for which H_0 1 is accepted, short-cut F test on ranges in median profiles (Appendix). Compare to ANOVA interaction 2 × 3.
5. Did community structure change coincident with the storm?	No relation between strength of rank correlation between two profiles and timing of these profiles with respect to the storm.	From abundances (m^{-2}) of each taxon in each profile, profiles are grouped by dendrogram based on rank correlation coefficients of abundances.

categories: A. Zooplankton; B. Phytoplankton and protozoa; C. Relations between zooplankton and phytoplankton; and D. Food for larval fish.

Figure 1 shows that the storm was not remarkable in the wind records from San Diego, but was quite apparent in the winds at San Clemente Island and in records of wave height at La Jolla and Oceanside. The generally lower wind speed and greater variability in speed and direction within each day at San Diego than at San Clemente Island are general phenomena (Dorman 1982). The wind at San Diego is probably more typical of the actual wind off Dana Point, while the San Clemente winds are more typical of the offshore condition generating the swell arriving there. Since the energy appearing as wind-induced turbulence increases as the cube of the wind speed, a doubling of wind speed increases turbulent energy eightfold.

Following the storm, surface temperatures and the thermal gradient in the upper 30 m were reduced at the sampling location off Dana Point, though the change in thermal gradient was not apparent until more than a day after the storm, and water temperatures at La Jolla were higher after the storm (Fig. 1). Minimal thermal gradients in the upper 30 m were also observed by the second vessel working at Dana Point on the night of 4-5 April. Though there was pronounced day-to-day variation in depths of isotherms, isotherms tended to be shoaler after the storm. For example, the poststorm median depths of 12°, 13°, and 14°C isotherms all were shoaler by 4.7-5.9 m than were the prestorm median depths (Pommeranz foot-

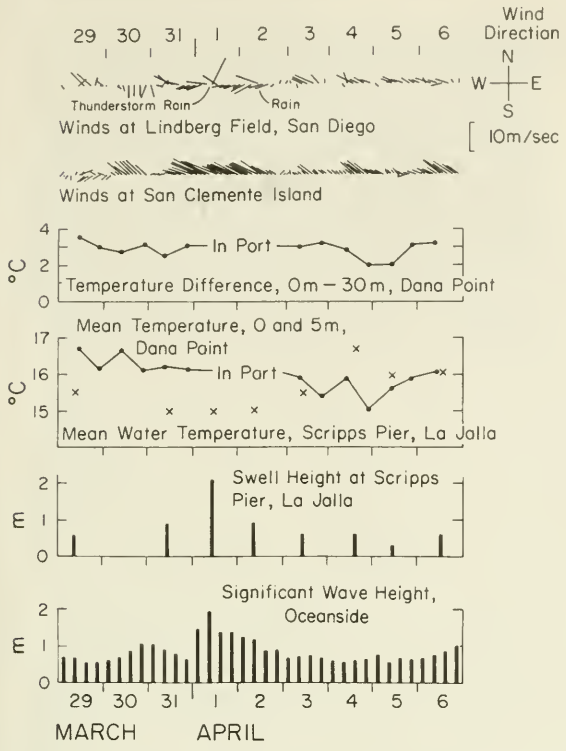

FIGURE 1.—Winds, water temperature, temperature gradient, and wave height at Southern California locations during this study. For temperature, dots are Dana Point, x's are La Jolla. Wind direction is the direction from which the wind is blowing.

note 3), and these differences were each significant by rank sum test ($P \leq 0.05$). This is not what one would expect from simple mixing, in which the nearsurface isotherms should shoal and the deeper isotherms deepen.

A. Zooplanktonic Taxa and Community Structure

We examined statistically the data on zooplankton summarized in the Appendix for answers to several questions concerning temporal changes in the distributions, using the ANOVA or nonparametric tests summarized in Tables 1 and 2. Daytime vertical distributions of many of these taxa off Southern California in late spring and fall are given by Fiedler (1983). As noted in the tables, there are potential ambiguities in the interpretation of even statistically significant results, such as the difficulty in distinguishing diel migration of a zooplanktonic taxon from a diel variation in its capability to avoid capture by the pump. More serious, and applicable to phytoplankton as well as zooplankton, is the impossibility of distinguishing between 1) biological changes caused directly by the storm (such as vertical redistribution, changes in behavior, or changes in the balance between birth and death of a taxon) and 2) storm-driven advection into the area of water with planktonic populations differing in abundances or behavior from those present prior to the storm, but neither the original nor the replacement populations having themselves changed in these properties. Advection undoubtedly occurred before, during, and after the storm; the issue is whether biologically caused changes associated with the storm occurred as well.

1. Diel Vertical Migrations

Based on results from ANOVA classification 1 (Table 1) or nonparametric Test 1 (Table 2), the taxa migrating into the upper 50 m from deeper water at night were the copepodites and adults of *Pleuromamma* and *Metridia*. These are real migrations, since sampling the water column of the Southern California Bight to greater depths reveals a change in depth of maximal abundance from below 100 m by day to within the upper 50 m at night (Esterly 1912; Enright 1977; Brooks and Mullin 1983). Euphausiid furcilia were also more abundant at night than by day.

Of the remaining zooplanktonic taxa (which did not have significant diel variation in total abundance within the upper 50 m), the populations of female, CV, and CIII *Calanus*, euphausiid calyptopes, and cyphonautes larvae were centered significantly higher at night than by day in the water column. Again, these results are consistent with results of sampling to greater depths in nearby waters (Esterly 1912; Enright and Honegger 1977; Mullin 1979; Brooks and Mullin 1983). Other taxa probably belonging to this category of behavior are adult *Rhincalanus* and *Eucalanus* (numbers too small for reliability). Curiously, when temporal changes are removed from the analysis (ANOVA classification 3 (Table 1)), female and CV *Calanus* and adult *Rhincalanus*, *Eucalanus*, and *Metridia* tend to be uniformly distributed in the upper 50 m.

2. Changes Following the Storm

Several taxa were significantly different in abundance following the passage of the storm [ANOVA classification 2 (Table 1) or nonparametric Test 3 (Table 2)], and most of these were larval

forms. *Acartia*, "*Paracalanus*", and "other" nauplii were significantly more abundant in 3-6 April samples than in the prestorm set (Fig. 2), while the abundance of larval fish in our samples decreased, as did that of adult and copepodid *Oithona*. An increase in abundance of appendicularians was almost significant. From the point of view of a larval or young juvenile fish, there were more items of desirable food (copepod nauplii and fewer siblings after the storm. No change was detected in those taxa (adult *Labidocera* and *Corycaeus*, chaetognaths) likely to be important zooplanktonic predators on larval anchovy.

Some of these changes appear to be continuations of trends evident before the storm (Fig. 2). However, the fact that larval copepods of several types were more abundant following the storm suggests that the storm directly or indirectly stimulated reproductive activity, though stimulation of hatching of benthic eggs (cf. Uye and Fleminger 1976; Landry 1978) or advection of populations from an area of greater fecundity

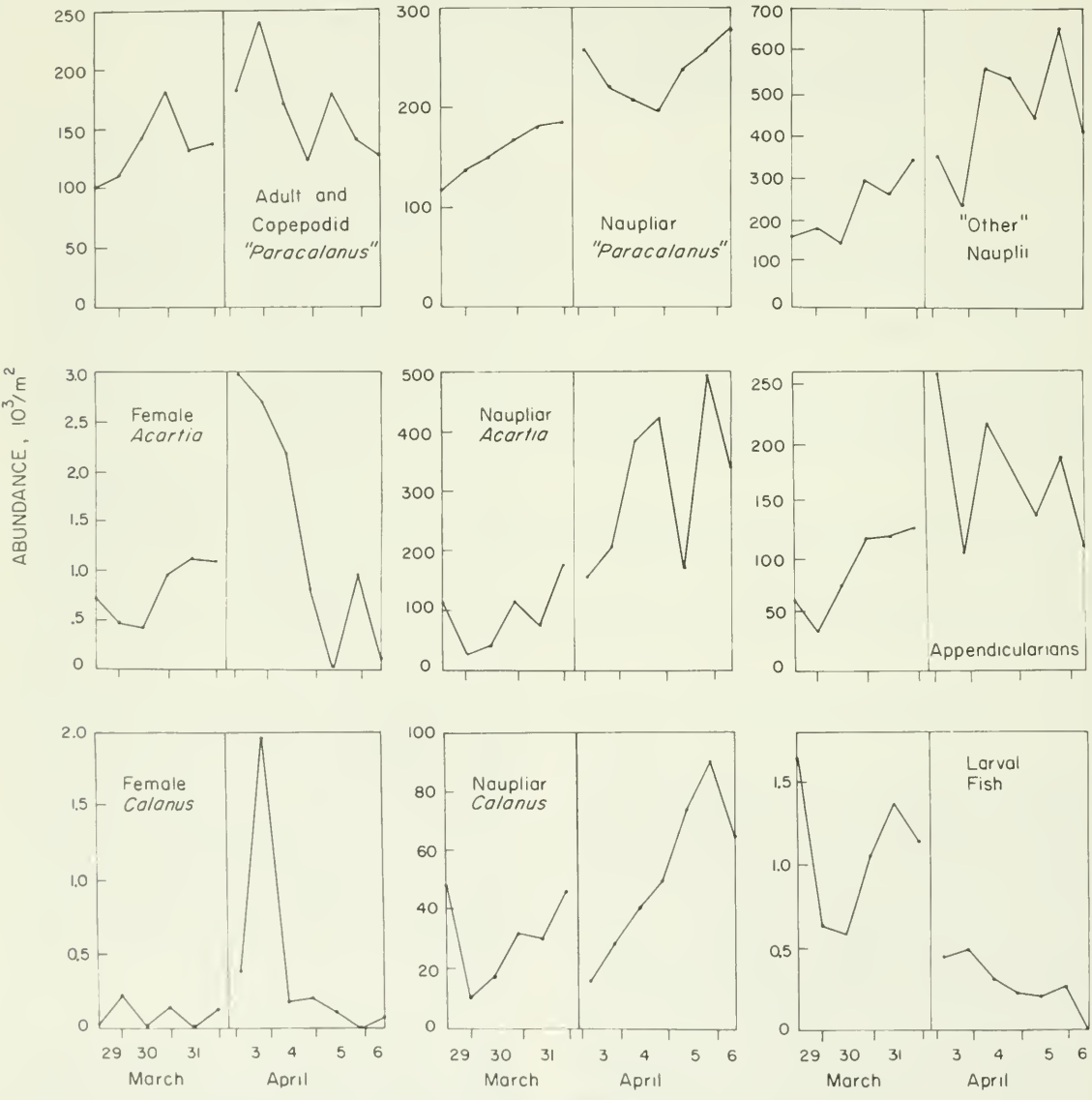

FIGURE 2.—Temporal change in total abundance (m^{-2}) of selected zooplanktonic taxa. The vertical line in each panel separates "prestorm" on the left from "poststorm" on the right. "*Paracalanus*" includes some *Clausocalanus* spp.

would give the same result. Given the naupliar life span of a few days, one would expect that, if reproduction were responsible, the ratio of nauplii to adults would continue to increase for the 3 d following the storm (though such a finding would not rule out advection). This is most readily tested for *Acartia* (nauplii/female) and "*Paracalanus*" (nauplii/adults and copepodites), since the older stages remained within the 0-50 m water column day and night (ANOVA classification 1 not significant). The ratio, nauplii/female, for *Acartia* increased dramatically; indeed, so much so that published values of maximal fecundity (50 eggs/female per day, Landry 1978; Uye 1981) are barely sufficient over the 5-d period including the storm (1-5 April) to account for the observed ratio on 6 April, even if no death or metamorphosis of nauplii occurred. This is because female *Acartia*, though unusually abundant immediately after the storm on 3 April, declined dramatically from that time until 6 April (Fig. 2). For "*Paracalanus*", which has approximately the same maximal fecundity as *Acartia* (Checkley 1980a), the ratio of nauplii to copepodites plus adults was slightly greater on 6 April than during the preceding 2.5 d. Evidence that the capacity of the environment to sustain reproduction of "*Paracalanus*" increased after the storm is presented in Section C below. Hence, the results are qualitatively consistent with the hypothesis that the storm stimulated reproduction, especially in *Acartia;* but other explanations cannot be ruled out. It is noteworthy, however, that no "exotic" taxa appeared after the storm.

Significance of ANOVA interaction 1 × 2 indicated that for two taxa (euphausiid furcilia and CV *Calanus*), the tendency to be more abundant in the upper 50 m at night than by day was more pronounced before the storm. Another migratory taxon—cyphonautes larvae—showed both a change in average depth distribution within the upper 50 m and a change in pattern of diel migration (significance in ANOVA interactions 2 × 3 and 1 × 2 × 3). The nighttime distributions of cyphonautes larvae were similar before and after the storm, but the daytime distribution was shifted to shallower water after the storm; adult *Corycaeus* showed the same (but nonsignificant) tendency, though they did not have a significant diel migration over the whole period (cf., evidence for a reverse migration by this species off Southern California in Fiedler 1983). *Pleuromamma* was virtually absent from the upper 50 m during the day both before and after the storm, but at night tended to occur shallower within this layer after the storm.

Diel migration was not detected in *Calanus* CII and CIII copepodites (ANOVA interaction 1 × 3 not significant), nor did they change significantly in total abundance after the storm (ANOVA classification 2 not significant). There was, however, a shoaling of the distributions of both stages both day and night after the storm (ANOVA interaction 2 × 3 significant). Larval fish were also shallower in our samples by day after the storm.

The vertical distributions of these three taxa were still stratified after the storm but were shifted with respect to depth. Another potential effect of the storm, which could also result in significance of ANOVA interaction 2 × 3, is homogenization of strongly stratified distributions into more nearly uniform ones. Reduction of the temperature gradient (Fig. 1) reinforces this possibility. The reverse process—an increase in stratification—is possible as a result of biological responses to the physical disturbance. Test 4 is a simple way to examine this question, though it is insufficient to detect some possible complex redistributions. The results of this test were contrary to expectation; only 2 taxa, *Labidocera* nauplii and copepodites, had greater ranges of abundance in the water column before the storm, while 13 taxa had greater ranges after the storm. Included in the latter group were *Acartia* and "other" nauplii, both of which increased in overall abundance after the storm, and all five juvenile copepodid stages of *Calanus*. Thus, as far as the zooplankton is concerned, poststorm stratification was generally more marked than that prestorm. It may be of significance, however, that the two taxa whose prestorm abundances were more strongly stratified than in the poststorm condition were taxa with strong neustonic (nearsurface) affinities (Barnett 1974; Appendix).

Inspection of the data (see Appendix) revealed several other taxa which appeared to have distributional changes of the sorts described above, though these were not significant by the criteria used in the statistical tests. This means that other sources of variability in abundance—notably, horizontal patchiness on the scales of a few kilometers, or vertical internal motions creating high variability at a fixed depth from day to day as water passed the sampling location—were more important than were those patterns of change the statistical tests were chosen to detect.

Finally, we can examine the overall similarities in the zooplanktonic community of the upper 50 m

(as abundances m^{-2}), excluding those taxa which significantly changed in total abundance in this layer from day to night. The weighted-pair dendrogram of Spearman's rank difference correlation coefficients (Fig. 3A) shows an imperfect separation into profiles taken before and after the storm, the first poststorm profile (#7) being more like those before the storm. This is evidence against the hypothesis that physical advection of new populations caused all the poststorm differences, though it is also possible that advection caused by the storm affected our site only after a delay. The storm's apparent effect on the thermal gradient (Fig. 1) was also delayed for some time. Even with some of the migrating taxa excluded, there is a partial separation in the dendrogram of nocturnal from diurnal profiles.

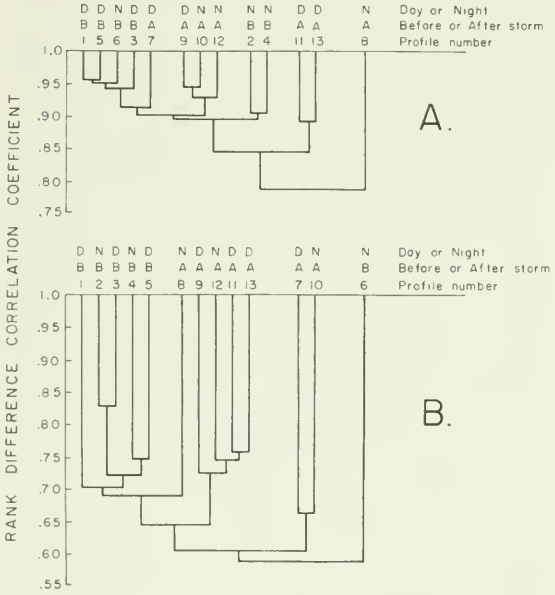

FIGURE 3.—Dendrograms of faunal (A) and floral (B) similarities of the upper 50 m of water off Dana Point, Calif. Faunal assemblages are based on 39 taxa, floral assemblages on 126 taxa (not just those listed in Appendix). "Floral" includes protozoans. All coefficients are significant at $P < 0.001$.

B. Chlorophyll, Phytoplankton, and Protozoa

Because of the mechanisms of feeding used to separate small particles of food from water, there are probably no strict herbivores among the zooplankton we studied, i.e., no animals which ingest living phytoplankton without also ingesting other particulate organic matter. Nevertheless, we used the distribution of chlorophyll (see Appendix) as the measure of the distribution of food for particle-grazing species; in the euphotic zone of the Southern California Bight, the concentration of chlorophyll is closely correlated with that of particulate organic carbon, with particulate ATP, and (within any one season) with the chlorophyll in particles >5 μm (Mullin and Brooks 1976; Eppley et al. 1977; Mullin 1979).

We had adequate data to answer Questions 1-4 from Table 2 for chlorophyll (= "taxon"). We used the phytoplanktonic and protozoan abundances from the physically integrated samples for all 13 profiles (see Methods) to perform Tests 1, 3, and 5 concerning the whole 50 m water column. We restricted Questions 2 and 4 to the upper 40 m (since these taxa were rare below this depth) and used data from five diurnal and three nocturnal profiles in answering these questions, since only those profiles were suitable for counting (see Methods). Only one of the nocturnal profiles was poststorm. In order to obtain estimates of "within classification" variability and still maintain a balanced design, we reduced the ANOVA to a two-way design, retaining "before vs. after storm" and "depth" as classifications. Thus, diurnal and nocturnal samples were considered replicates (there was no evidence of diel migration in the phytoplanktonic taxa). We again restricted the analysis to the upper 40 m. Variances of log-transformed data for these taxa were all homogeneous in the four profile data set (profiles 5, 6, 9, and 10). Thus we applied the ANOVA to a subset of those profiles suitable for nonparametric tests.

The concentration of chlorophyll per m^2 did not change from day to night (H_0 1 accepted), nor did the vertical distribution of chlorophyll within the upper 50 m change from day to night (H_0 2 accepted). The median chlorophyll concentration (m^{-2}) was greater after the storm, but not significantly so by Test 3. Vertical profiles of in vivo fluorescence of chlorophyll and samples of phytoplankton from the fluorescence maximum layer (cf. Kiefer and Lasker 1975; Cullen et al. 1982) were taken from the second ship working concurrently at Dana Point. Comparison of the integrated fluorescence profiles indicated that this measure of chlorophyll increased significantly after the storm ($P < 0.01$ by a variant of Test 3).

Inspection of the data (see Appendix) indicated a shoaling of the chlorophyll maximum layer after the storm, and this was significant by a Mann-Whitney U test for differences in depth of occur-

rence of the median value before vs. after the storm. This tendency was also shown by isotherms (see above). The range of concentrations of chlorophyll in the water column tended to increase, meaning that chlorophyll maxima were accentuated after the storm, though hypothesis 4, based on the median profiles, was not rejected ($0.01 < P < 0.025$).

No phytoplanktonic or protozoan taxa we examined migrated dielly into and out of the upper 50 m nor did any taxon migrate dielly within the upper 40 m. The two-way ANOVA of four profiles detected significant decreases in poststorm abundances of the diatoms *Nitzschia* spp., *Bacteriastrum* spp., *Rh. alata*, and *Rh. fragilissima*; all but the last of these decreases were also significant by nonparametric Test 3 applied to the full 13-member set of integrated profiles. This latter test also revealed a significant decrease in poststorm abundance of another diatom, *S. costatum*. Only the dinoflagellate, *Prorocentrum*, was more abundant after the storm by the ANOVA test. When the data set of 13 integrated profiles was examined by nonparametric Test 3, significant increases were also detected in the poststorm abundance of *Lohmanniella* (a potential larval fish food) and *Ceratium* spp. Neither *Gymnodinium splendens* nor *Cochlodinium catenatum* (two potential food items for larval anchovy) changed significantly in abundance in samples taken at the depth of the fluorescence maximum layer from the second vessel. The large diatom category, *Chaetoceros* spp., did not change in total abundance, but the species comprising this category changed at the time of the storm; in particular, *Ch. constrictus* was the dominant member of the genus after the storm, but was not encountered in the prestorm samples.

From the ANOVA, no phytoplanktonic taxa had poststorm vertical distributions different from their prestorm ones, when the criterion of $P \leq 0.01$ was used for significance, and only *Rh. alata* and *Prorocentrum* had significant changes as defined by $P \leq 0.05$. Hence, as far as we could tell from the four profiles which were usable in the ANOVA, the storm had much less effect in changing the vertical distributions of specific phytoplankters (and protozoans) than it did for zooplankton. This conclusion is, however, suspect (see below).

Nonparametric Test 4, for which eight profiles were usable, indicated that the poststorm range of abundances in the upper 40 m was greater than the prestorm range for five of the dinoflagellate taxa, *Mesodinium rubrum*, and *Lohmanniella*, while *Nitzschia*, *Rh. fragilissima*, and *S. costatum* had significantly smaller poststorm ranges. These eight profiles strongly suggested poststorm shoaling of the vertical distributions of the potential food species, *C. catenatum*, *G. splendens*, and *Laboea*, but the data sets were too small to establish statistical significance at $P \leq 0.01$.

The general changes associated with the storm were therefore decreases in the abundances and in the degree of stratification of some diatoms, and increases in abundances and degree of stratification of some dinoflagellates and protozoans. However, significant changes in the pattern of stratification with depth were more difficult to detect because of the reduced data sets, except for the shoaling of the distribution of chlorophyll.

The floral composition of the profiles permitted a clear separation into prestorm and poststorm assemblages, with the exception of the last prestorm profile, which was quite different from the others (Fig. 3B). This result was different from the analysis of zooplankton (Fig. 3A), where the first poststorm profile was unexpectedly grouped with prestorm profiles. Both results, however, indicate that the compositional changes associated with the storm were gradual rather than abrupt. Unlike the faunal assemblages, the floral grouping showed no tendency to separate day from night. The difference in correlation coefficients between dendrograms A and B probably reflects the fact that quite different numbers of taxa were counted, and that samples were counted by different techniques, rather than any fundamental distinction between phytoplanktonic and zooplanktonic assemblages.

C. Relations Between Zooplankton and Phytoplanktonic Biomass

If positive correlations between the abundances of particle-grazing zooplanktonic taxa and chlorophyll existed before the storm, it is reasonable to hypothesize that such correlations would be weaker or nonexistent after the storm due to turbulent disruption of associations.

We examined the following taxa of zooplankton in this regard, sometimes combining categories from the Appendix: Naupliar *Acartia*, naupliar *Calanus*, naupliar *"Paracalanus"*, copepodid and adult *Acartia*, CI-CIV *Calanus*, CV and female *Calanus* (nocturnal only), copepodid and adult *"Paracalanus"*, adult *Metridia* (nocturnal only), adult *Pleuromamma* (nocturnal only), and the appendicularians. We grouped data into four sets of profiles: three diurnal, prestorm; three noc-

turnal, prestorm; three diurnal, poststorm (excluding the 6 April profile); and three nocturnal, poststorm. In order to give each profile within a set equal weight and to restrict attention to vertical relations, we arranged data from each profile in order of increasing concentration of chlorophyll; next ranked the samples in order of increasing abundance of the taxon of interest; then calculated the Kendall's tau coefficient as a measure of correlation between that taxon and chlorophyll within each profile; and finally calculated the coefficient of concordance between the rearranged ranks of the taxon in the three profiles of a set as a measure of agreement on a common tendency (see Mullin and Brooks 1972). We then defined a persistent relation between a taxon and chlorophyll in one full set of profiles as requiring a significant ($P \leq 0.05$) concordance between the individual profiles of the set, tau coefficients of all profiles of the same sign (positive or negative), and at least one of the tau coefficients significant ($P \leq 0.05$).

No persistently negative relations were found between any taxon and chlorophyll in any set of profiles. In the diurnal, prestorm set, naupliar *Acartia*, naupliar *Calanus*, copepodid and adult *Acartia*, and appendicularians were all positively related to chlorophyll, and CI-CIV *Calanus* tended in this direction. These relations all vanished at night by our criteria, though naupliar *Calanus* tended to retain a positive association. After the storm, the strength of the diurnal, positive relations of naupliar *Acartia,* copepodid and adult *Acartia*, CI-CIV *Calanus*, and appendicularians increased, and naupliar *"Paracalanus"* also had a positive relation. At night after the storm, all taxa except naupliar *"Paracalanus"*, CV and adult *Calanus, Metridia*, and *Pleuromamma* had positive relations with chlorophyll. Thus, contrary to expectations, after the storm there were more positive relations between these particle-grazing taxa and the concentration of their food, measured as chlorophyll.

We reached a similar conclusion for the ciliates, *Laboea* and *Lohmanniella*; neither were persistently related to the vertical distribution of chlorophyll before the storm, but both were positively related after the storm by our criteria. Since fewer profiles for these protozoans were counted, we did not separate night from day in searching for the correlations.

Such correlations can also show seasonal variability; for example, Fiedler (1983) found strongly positive correlations between the vertical distributions of chlorophyll, *Paracalanus*, and *Penilia avirostris* (a cladoceran) in October, but strongly negative correlations between these zooplankters and chlorophyll in May; *Ctenocalanus vanus* showed a seasonal reversal of its relation to chlorophyll in the opposite direction.

In spite of the increased correlation after the storm between particle-grazers and their food, there is some evidence that the poststorm grazing pressure on phytoplankton was less than that prestorm. The ratio of chlorophyll to phaeopigments in the water column is an indicator of the ratio of living phytoplankton to the fecal material of grazers, and hence is inversely related to the grazing pressure per unit phytoplanktonic crop (Lorenzen 1967). The chlorophyll/phaeopigment ratio was significantly greater ($P < 0.05$ by rank sum test) after the storm, indicating a reduction in grazing relative to the available crop.

We derived a second indicator of the effect of the storm on relations between phytoplankton and zooplankton from a study of egg production of the copepod, *Paracalanus parvus*, and chlorophyll and particulate nitrogen in the Southern California Bight (Checkley 1980b). Checkley found that the nitrogen in phytoplankton was the best measure of fecundity-stimulating food, that about half the chlorophyll retained on a fiberglass filter was in particles >5 μm, and that the weight ratio of nitrogen in phytoplankton to chlorophyll was 12. From these relations, the egg production of *Paracalanus* is food-limited where the concentration of total chlorophyll is below 1.3 μg/l. By this standard, only 18% of the upper 50 m contained sufficient food for maximal egg production prior to the storm, while 34% of the water column met this criterion afterwards.

This conclusion is likely to be qualitatively correct unless the size distribution of phytoplankton was altered markedly by the storm, or the breadth of the copepods' diet with respect to nonphytoplankton was changed. Neither of these sources of error is particularly likely, since the ratio of >5 μm to total chlorophyll agrees with earlier results in the Bight (Mullin and Brooks 1976) and since the range of the data from which Checkley deduced the importance of chlorophyll in regulating egg production included all but one of the concentrations of chlorophyll we measured.

Further, the vertical distribution of adult and copepodid *"Paracalanus"* was positively correlated with that of chlorophyll after the storm and at night (see above). If this finding applies to female *"Paracalanus"* by themselves, a consider-

ably greater fraction of total reproduction occurred at maximal (i.e., nonfood-limited) rates after the storm.

A similar quantitative example of augmentation of zooplanktonic nutrition related to the storm can be calculated for CIV-adult *Calanus*, though the vertical distribution of these stages was not well correlated with that of chlorophyll. In June 1980, Cox et al. (1983) estimated the carbon budget of *Calanus* at various stations and depths in the Southern California Bight, and concluded that gain in biomass of these copepods was possible where the concentration of chlorophyll exceeded 0.9 μg/l. By this standard, the fraction of the upper 50 m where some growth was possible (nighttime only, because of diel migration) was 36% before and 58% after the storm.

A third test of the significance of vertical distributions and the effect of the storm on them was based on the plant pigments in the guts of the large copepods caught at various times and depths. The measurement of fluorescence of gut contents can be used as a quantitative estimate of the rate of ingestion of plant material if the breakdown of pigment, the gut passage time, and the background fluorescence due to an animal's own pigmentation are known (Mackas and Bohrer 1976). We chose to ask two simpler questions based on changes in fluorescence: 1) Were the total gut pigments (chlorophyll + phaeopigments) of copepods caught at specific depths correlated with the concentration of chlorophyll measured at the same depths, before or after the storm or both? 2) Did the amount of gut fluorescence of a taxon, independent of specific depths, change coincident with the storm? The first question addresses the issue of whether the copepods can be shown to have fuller guts at depths where phytoplanktonic food (as measured by chlorophyll) is more concentrated. If copepods move frequently from the depths at which they feed, such correlations would be difficult to establish (cf. Dagg and Wyman 1983). The second question is the more general one of whether the copepods were better nourished after the storm.

We tested data concerning female *Acartia*, female and CV *Calanus*, female *Metridia*, and female *Pleuromamma* in this regard, with 6-28 pre- or poststorm data points per taxon. Of these taxa, only *Acartia's* abundance was significantly positively associated with the vertical distribution of chlorophyll (see above).

The gut pigment per *Acartia* showed no relation to the ambient concentration of chlorophyll, however, while that of *Pleuromamma* was positively correlated with chlorophyll. In no case was the poststorm correlation (tau coefficient) between gut fluorescence and chlorophyll stronger than that prestorm. Hence, we could not show that for these taxa the distribution of degree of satiety became more strongly associated with the vertical distribution of chlorophyll after the storm, even though the range of chlorophyll concentrations available in the upper 50 m had increased.

Nor for any of these taxa was the poststorm amount of gut fluorescence significantly greater than that prestorm. Based on comparison between field-caught female *Acartia* and *Calanus*, and these same taxa fed to excess or starved in the laboratory, we conclude that both these populations were well fed in general both before and after the storm, and animals had plant food in their guts at all depths sampled. Hence, we could not demonstrate a change in nutritional status of the taxa as a result of the storm, even though the overall concentration of chlorophyll increased. All these taxa have been shown to feed on nauplii as well as phytoplankton (e.g., Haq 1967; Lonsdale et al. 1979; Landry 1981), but we could not test whether their nutrition from animal sources had improved coincident with the increase in abundance of nauplii following the storm.

D. Abundance and Vertical Distribution of Food for Larval Fish

Because larval fish are visual predators, it is the diurnal distributions of potential prey which are particularly relevant. Different species select (or are physically able to ingest) different prey, and of course different types of prey differ in their catchability, digestibility, and nutritive value. We will consider the distributions of food for two prototypical larvae representing extremes in a continuum of actual types. One is a small-mouthed larva which we will call "anchovy-like", based on Berner (1959), Lasker et al. (1970), O'Connell and Raymond (1970), Arthur (1976), and Lasker and Zweifel (1978). For these larvae, "large" prey consists of all copepod nauplii and lamellibranch and cyphonautes larvae (Appendix); "small" prey consists of all ciliates and all nonthecate, large dinoflagellates. Laboratory studies suggest the critical concentrations for both good survival and rapid growth are $\geq 5 \times 10^3$ large or $\geq 5 \times 10^4$ small prey l^{-1}, or an equivalent combination.

The other prototypical larva has a larger mouth and is more active; based on Arthur (1976), Hunter

and Kimbrell (1980), Lipskaya (1982), and Devonald (1983), this larva is "mackerel-like" (though *Scomber* and *Trachurus*, especially the latter, tend to spawn farther offshore than our sampling location). This larva requires a much lower concentration of "large" prey, 50 l^{-1}, and a large number of zooplanktonic taxa are potential food: all copepod nauplii; lamellibranch and cyphonautes larvae; *Acartia, Labidocera, Metridia,* and *Pleuromamma* immature copepodites; *"Paracalanus", Oithona, Euterpina, Corycaeus, Oncaea,* and *Microsetella* copepodites and adults; euphausiid nauplii and calyptopes; CI, CII, and CIII *Calanus*; "other copepods"; cladocerans; and (see Lipskaya 1982) appendicularians. Nauplii and lamellibranch and cyphonautes larvae are considered small prey, the remainder being large. This spectrum of prey is also appropriate for young postlarval anchovy.

Figure 4 shows the prestorm and poststorm diurnal vertical distributions of food for the two prototypical larval types, in terms of the equivalent "large prey" for each; the figure legend gives the conversion factors used. In no instance was the laboratory-determined critical concentration of prey exceeded. We do not believe that this conclusion is due to destruction of prey during preservation.

We tested hypotheses concerning the vertical stratification and the effect of the storm on distributions of prey by two-way ANOVAs on log-transformed abundances from the diurnal profiles (3, 5, 7, and 9) similar to those used for phytoplanktonic taxa (Section B above), since variances were homogeneous by Barlett's test. We used our data on the diurnal abundances of total larval fish to examine correlations with the food of "anchovy-like" larvae by means of the tau coefficient for these profiles.

It is apparent from Figure 4A that "small prey" dominated the food supply for "anchovy-like" larvae, even when expressed as its equivalence in terms of large prey. Because this category had not increased significantly after the storm, neither had total prey for these larvae; however, large prey were both more abundant and more strongly stratified.

The food supply of "mackerel-type" larvae was

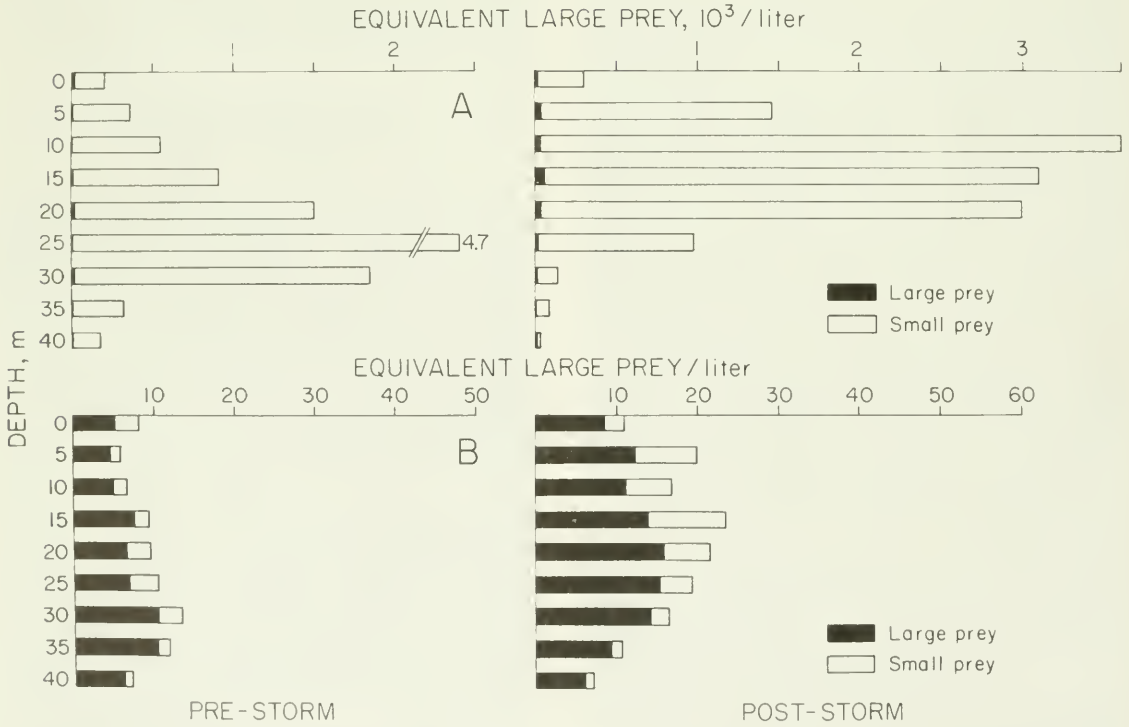

FIGURE 4.—Median vertical, diurnal distributions of larval fish food, as "equivalent large prey", before and after the storm. Taxa comprising categories of prey are listed in text. A. Prey of "anchovy-like" larvae. Graphed concentrations of small prey are 0.1× actual concentrations. B. Prey of "mackerel-like" larvae. Graphed concentrations of small prey are 0.2× actual concentrations.

dominated by "large" rather than "small" prey. That these types of zooplankters are less abundant very near surface and below 30 m than at intermediate depths is apparently not unusual in spring (Fiedler 1983:fig. 5). Both types of prey were more abundant after the storm. Total food for both types of larvae tended to be concentrated nearer the surface in the poststorm condition.

Although the numbers of larval fish in our samples are too small, especially after the storm, to provide a strong test of spatial correlation with their food supplies, the tau coefficients of correlation between total larval fish and their food by day were positive in all cases, but somewhat less so after the storm for the nonthecate dinoflagellates and ciliates which dominated the food supply of "anchovy-like" larvae. This was the case even though the poststorm distributions of both larval fish and food were concentrated nearer the surface than were the prestorm distributions.

SUMMARY AND DISCUSSION

We concentrated during this study on the consequences of the vertical distributions of plankton for the production of zooplanktonic food for larval fish, and on the differences in distributions of food experienced by larval fish at one coastal location before and after a small storm. Since advection surely occurred, we do not intend to imply that the same individual larvae experienced both sets of conditions.

Conclusions we believe to be ecologically significant and statistically verified are as follows:

1. The biotic environment was vertically structured.
   a. Of the 28 zooplanktonic taxa for which the ANOVA was appropriate, 22 had a consistently uneven (i.e., stratified) pattern of distribution with depth in the upper 50 m. Of the remaining six taxa, three had regular temporal changes in vertical distribution. Hence, only 3 of the 28 taxa were uniformly distributed both vertically and dielly.
   b. Chlorophyll was stratified in the upper 50 m, and 9 of the 18 phytoplanktonic-protozoan taxa examined had stratified distributions in the upper 40 m; the stratified taxa were notably dinoflagellates and the oligotrich ciliates rather than the diatoms.
   c. Both small prey and total prey for "anchovy-type" larvae were vertically stratified, but prey for "mackerel-type" larvae was not.
   d. Though the abundance of *Acartia* was correlated vertically with that of chlorophyll, its gut fullness was not.
2. Several features were different after the storm.
   a. Several zooplanktonic taxa—notably, various nauplii—were more abundant, while larval fish were less so. *Ceratium, Prorocentrum,* and *Lohmanniella* had increased, while several diatoms had decreased. Evidence suggested a poststorm increase in chlorophyll, but contained ambiguities.
   b. Several zooplanktonic taxa—*Pleuromamma* at night, cyphonautes by day, *Calanus* CII and CIII, larval fish—tended to be concentrated in shallower depths after the storm, as did chlorophyll, but data were insufficient to show that the large-sized phytoplanktonic taxa we studied responded in this way. Food for both types of larval fish was concentrated in shallower water after the storm. The neustonic distribution of *Labidocera* nauplii and copepodites was less pronounced after the storm, but in general the poststorm vertical stratification was at least as great as that prestorm, even though the temperature gradient was lessened. This general conclusion was also true for phytoplankton (except for some diatoms which were less abundant after the storm) and for the sum of forms representing "large food" for "anchovy-like" larvae and "small food" for "mackerel-like" larvae.
3. Relations between predators and prey were different following the storm.
   a. Several taxa maintained or established abundant populations in those parts of the water column where food was most plentiful. However, this was not true for taxa with pronounced diel vertical migrations. The estimated poststorm reproduction of *"Paracalanus"* was less limited by food than was the prestorm reproduction, and *Calanus* could obtain sufficient food for growth in a greater fraction of the water column after the storm; but we could not demonstrate a poststorm increase in gut fullness of large herbivores.
   b. Larval fish, both those categorized as "anchovy-like" and "mackerel-like", also were exposed to augmented concentrations of their respective "large" food items, both immediately and perhaps as a result of en-

hanced growth and reproduction of zooplankton and reduced competition from other larvae. However, the supply of food for larvae was less than that thought necessary for rapid growth and high survival, and the spatial association between total larvae and abundant, small food (dinoflagellates and protozoans) was slightly less strong after the storm; this category of food was not significantly more abundant after the storm.

Lacking information on the planktonic stocks and their distribution, we might have hypothesized that the decrease in abundance of larval fish following the storm (Fig. 2) was due to starvation because the storm-induced turbulence homogenized the vertical distributions of food. The results shown in Figure 4 make this hypothesis untenable.

Even though we did not find concentrations of food exceeding laboratory-determined thresholds for growth, certainly the most important conclusion with respect to the storm from the point of view of a larval fish is that there was as much food available after the storm and that copepod nauplii (which laboratory studies have shown to be desirable prey) increased significantly. In view of this, we predict that the larvae present after the storm were growing faster (or starving more slowly), were in better condition, and were more likely to have food in their guts than those present before the storm, even though the latter were the more numerous. Also, since the available food increased at several depths in the water column, we predict that the occurrences of well-nourished anchovy larvae (if any were present) should be shallower after the storm and less strictly confined to one or two depth strata.

A tendency for larvae to be less closely associated after the storm with layers of abundant dinoflagellates and ciliates might negate this prediction; the nature of the vertical relations should now be examined using the more reliable distributions of larvae determined by a towed opening-closing net. Another condition which would result in failure of our prediction is if the larvae actually rely for nutrition on micropatches of food, such as organic aggregates and an associated assemblage of phytoplankton and microzooplankton (e.g., Alldredge 1976; Silver et al. 1978). Devonald (1983) has suggested this for larvae of jack mackerel, *Trachurus symmetricus*, farther offshore in the Southern California Bight. If this is true, sampling on the scale of hundreds of liters, as we did, would not detect the redistribution of food on the scale most important for larval survival and growth; storm-induced turbulence could have disrupted such micropatches, making the supply of food less rather than more favorable. A large amount of true microscale sampling, such as that done by Owen (1981), would then be required to predict correctly the effect of the storm on the larvae.

ACKNOWLEDGMENTS

We thank R. Lasker, G. Moser, and R. Owen of the National Marine Fisheries Service for collaboration in this project. J. Star and P. Peterson assisted with sampling, as did D. Carlson, owner and operator of the *Fisherette*. D. Cayan and R. Seymour supplied some of the wind and wave data. This long after the fact, we thank Neptune for the storm. E. Venrick made helpful comments on the manuscript (especially in its statistical aspects), and D. Osborn typed it several times. Financial support was from the Department of Energy, DE-AT03-82-ER60031, and ship funds from the Marine Life Research Group.

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APPENDIX

Vertical Distribution of Taxa

APPENDIX TABLE 1.—Diurnal profiles before storm. * = variances heterogeneous; ANOVA not used.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON	median number per cubic meter										
Naupliar *Acartia*	75	407	786	1,533	5,074	1,345	448	78	0	39	49
Naupliar *Labidocera*	11,688	325	75	77	70	67	34	0	0	0	0
*Naupliar "*Paracalanus*"[1]	2,397	3,004	2,000	1,529	1,761	2,941	8,679	3,333	1,418	1,023	1,478
*Naupliar *Calanus*	693	956	597	536	515	1,070	299	107	75	79	33
Naupliar *Rhincalanus*	0	0	0	77	7	252	163	71	7	4	0
*Other nauplii	1,653	1,832	3,283	4,138	7,647	2,809	5,000	2,679	3,060	1,732	1,569
Female *Acartia*	4	22	23	19	21	8	4	0	0	0	0
Male *Acartia*	4	11	19	23	11	0	0	0	0	0	0
Copepodite *Acartia*	12	18	302	284	345	147	0	0	0	0	0
*Adult *Labidocera*	0	0	0	0	0	0	0	0	0	0	0
*Copepodite *Labidocera*	1,571	234	4	0	0	0	0	0	0	0	0
Adult and copepodite "*Paracalanus*"[1]	3,117	2,711	2,239	1,456	1,029	840	3,051	4,783	3,694	2,598	1,814
*Appendicularians	285	1,245	1,214	3,218	1,985	4,622	2,164	856	67	24	25
*Adult and copepodite *Oithona*	0	293	970	1,116	2,746	1,070	1,661	1,739	521	736	1,100
Adult and copepodite *Euterpina*	9	0	71	284	662	602	293	107	0	0	0
Euphausiid nauplii	0	0	11	0	4	0	3	11	16	4	13
*Euphausiid calyptopis	0	0	4	17	14	30	4	23	7	8	5
Euphausiid furcilia	0	0	4	0	4	20	7	31	8	12	14
Chaetognaths	11	163	204	307	121	172	97	43	16	35	31
Female *Calanus*	0	0	0	0	0	0	0	0	0	0	0
Male *Calanus*	0	0	0	0	0	0	0	0	0	0	0
C V *Calanus*	0	0	0	0	0	0	0	0	0	3	0
C IV *Calanus*	0	0	0	0	0	4	4	4	8	0	14
C III *Calanus*	0	0	0	4	0	3	8	14	15	4	5
C II *Calanus*	0	4	0	4	7	8	57	21	0	3	0
C I *Calanus*	0	8	4	0	13	13	57	18	4	0	0
*Adult *Corycaeus*	15	33	79	87	92	97	157	74	92	67	64
*Adult and copepodite *Oncaea*	83	73	38	230	70	168	2,463	2,536	1,679	1,299	1,225
Microsetella	0	4	4	843	1,513	1,271	305	286	65	173	196
Adult *Metridia*	0	0	0	0	0	0	0	0	0	0	0
*Adult *Pleuromamma*	0	0	0	0	0	0	0	0	0	0	0
*Copepodite *Metridia* and *Pleuromamma*	0	0	0	0	0	0	0	12	22	91	163
*Adult *Rhincalanus*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Rhincalanus*	0	0	0	0	0	0	34	18	15	17	15
*Copepodite *Eucalanus*	0	0	0	0	0	0	0	25	0	0	0
Other copepods	0	0	15	0	0	0	75	11	7	0	3
Fish eggs	43	29	18	8	7	3	0	0	0	0	0
Fish larvae	0	0	30	74	59	57	23	7	0	0	0
Cladocerans (*Evadne*)	50	121	86	12	0	4	0	0	0	0	0
Polychaete larvae	0	22	104	92	56	104	78	51	28	22	21
Lamellibranch larvae	0	0	0	0	0	0	0	0	0	104	0
Cyphonautes larvae	0	0	0	0	0	0	52	140	116	30	0
*CHLOROPHYLL	median micrograms per liter										
	0.33	0.36	0.44	0.63	0.97	1.03	2.06	0.77	0.49	0.32	0.28
PHYTOPLANKTON + CILIATES	median number per 100 ml										
Nitzschia spp. S	1,627	946	2,412	1,536	2,326	987	1,369	1,008	261		
Bacteriastrum spp. (chains)	56	86	84	78	78	95	66	54	16		
Chaetoceros spp.	2,488	3,845	4,307	3,246	3,576	1,427	4,270	1,764	413		
Rhizosolenia alata	112	116	90	86	80	35	18	4	2		
Rhizosolenia fragilissima	98	120	156	120	268	53	6	0	8		
Skeletonema costatum	78	56	18	96	76	24	3	88	40		
Ceratium spp.	42	30	24	32	14	11	54	4	0		
Gonyaulax polyedra/polygramma	26	14	16	20	12	15	14	0	0		
Prorocentrum sp. C	0	0	2	4	94	34	0	0	0		
Protoperidinium spp.	26	30	26	20	18	7	22	2	4		
Cochlodinium catenatum	50	56	290	714	1,272	4,065	1,182	148	68		
Gymnodinium splendens	0	0	0	2	0	341	300	0	0		
Torodinium robustum	30	26	20	10	0	16	12	0	0		
Umbilicosphaera sibogae	50	52	42	34	44	0	18	4	0		
Emiliania huxleyi	1,213	1,821	1,822	1,298	1,883	1,928	927	2,489	1,152		
Mesodinium rubrum	8	2	6	8	2	8	4	8	14		
Laboea spp.	30	146	110	74	82	104	124	72	36		
Lohmaniella spp.	68	128	116	94	134	154	218	78	50		

[1]Includes some *Clausocalanus*.

APPENDIX TABLE 2.—Diurnal profiles after storm.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON	median number per cubic meter										
Naupliar *Acartia*	1,834	8,333	10,525	21,954	6,583	1,867	197	153	60	0	57
Naupliar *Labidocera*	1,600	4,679	0	0	0	0	0	0	0	0	0
Naupliar "*Paracalanus*"[1]	2,644	10,114	3,669	5,576	7,219	7,810	5,015	1,651	972	888	1,115
Naupliar *Calanus*	950	810	424	2,180	1,833	837	456	391	193	128	196
Naupliar *Rhincalanus*	0	631	0	95	134	9	204	228	0	36	124
Other nauplii	2,740	14,601	15,091	18,210	14,232	8,216	5,327	3,990	3,414	2,570	1,927
Female *Acartia*	0	5,666	69	9,736	6,617	3,994	0	1,907	0	0	0
Male *Acartia*	0	5,645	27	14	6,617	7	0	0	0	0	0
Copepodite *Acartia*	36	643	1,758	1,756	1,807	288	0	1,905	1,903	0	0
Adult *Labidocera*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Labidocera*	153	79	7	0	0	0	0	0	0	0	0
Adult and copepodite "*Paracalanus*"[1]	5,646	6,200	1,726	1,796	2,279	4,808	6,434	3,090	1,371	660	435
Appendicularians	3,053	3,165	3,551	5,785	8,364	5,651	1,746	754	122	79	44
Adult and copepodite *Oithona*	21	696	391	983	814	1,617	1,953	1,044	730	567	516
Adult and copepodite *Euterpina*	5	229	1,196	2,358	962	190	80	23	0	25	0
Euphausiid nauplii	0	0	171	0	214	9	19	33	27	26	25
Euphausiid calyptopis	0	13	11	89	41	38	21	20	15	9	14
Euphausiid furcilia	0	0	12	15	23	36	27	28	19	16	20
Chaetognaths	8	164	511	251	190	60	42	24	12	6	12
Female *Calanus*	0	0	0	0	0	0	0	22	8	8	4
Male *Calanus*	0	0	0	0	0	0	0	20	4	0	4
C V *Calanus*	0	0	0	116	0	11	12	18	12	0	4
C IV *Calanus*	0	68	0	119	45	16	32	6	0	8	0
C III *Calanus*	0	0	0	119	90	43	14	8	0	0	0
C II *Calanus*	7	0	297	27	50	46	11	0	0	0	0
C I *Calanus*	7	79	303	15	31	25	12	0	0	0	0
Adult *Corycaeus*	20	107	337	305	478	74	87	69	48	46	43
Adult and copepodite *Oncaea*	0	711	255	215	707	2,678	3,466	2,011	1,797	1,322	1,204
Microsetella	14	40	719	476	45	171	236	190	23	37	33
Adult *Metridia*	0	0	0	0	0	0	0	0	0	0	0
Adult *Pleuromamma*	0	0	0	0	0	0	0	1,047	0	0	0
Copepodite *Metridia* and *Pleuromamma*	0	0	0	0	0	0	81	153	176	135	115
Adult *Rhincalanus*	0	0	0	0	0	0	0	0	97	80	0
Copepodite *Rhincalanus*	0	0	0	0	30	31	57	8	99	80	6
Copepodite *Eucalanus*	0	0	0	0	23	16	0	7	97	80	0
Other copepods	0	0	0	15	0	17	6	8	10	0	6
Fish eggs	14	18	19	89	0	0	0	0	0	0	0
Fish larvae	0	11	15	95	19	0	0	0	0	0	0
Cladocerans (*Evadne*)	164	273	101	102	16	0	0	0	0	0	0
Polychaete larvae	0	100	294	193	375	256	181	101	52	33	19
Lamellibranch larvae	0	0	0	0	0	54	195	138	0	0	0
Cyphonautes larvae	0	193	20	36	15	58	0	8	0	0	0
CHLOROPHYLL	median micrograms per liter										
	0.74	1.08	2.30	2.91	2.05	0.86	0.62	0.52	0.36	0.31	0.21
PHYTOPLANKTON + CILIATES	median number per 100 ml										
Nitzschia spp. S	87	48	0	0	0	0	0	130	0		
Bacteriastrum spp. (chains)	0	20	24	8	4	4	4	12	0		
Chaetoceros spp.	7,957	3,186	265	1,416	1,099	696	87	565	174		
Rhizosolenia alata	28	24	8	16	8	0	0	0	0		
Rhizosolenia fragilissima	44	16	36	8	4	0	0	0	0		
Skeletonema costatum	0	0	0	0	0	0	0	0	24		
Ceratium spp.	64	80	72	104	56	0	0	4	0		
Gonyaulax polyedra polygramma	16	56	88	32	16	0	0	0	0		
Prorocentrum sp. C	20	4	681	784	296	4	0	4	0		
Protoperidinium spp.	48	64	72	40	16	4	0	0	0		
Cuchlodinium catenatum	52	368	1,837	1,672	1,720	680	56	52	4		
Gymnodinium splendens	0	0	672	583	320	4	0	0	0		
Torodinium robustum	24	24	26	28	8	0	0	0	0		
Umbilicosphaera sibogae	0	104	40	56	32	4	0	0	0		
Emiliania huxleyi	1,681	1,504	3,009	1,858	609	1,130	696	1,478	973		
Mesodinium rubrum	16	24	32	16	8	0	0	0	0		
Laboea spp.	52	464	326	184	204	116	32	20	4		
Lohmaniella spp.	148	520	580	566	616	152	36	16	6		

[1]Includes some *Clausocalanus*

APPENDIX TABLE 3.—Nocturnal profiles before storm.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON	median number per cubic meter										
Naupliar *Acartia*	352	315	4,286	5,874	6,723	1,992	0	43	0	0	0
Naupliar *Labidocera*	1,636	870	75	0	0	0	0	0	0	0	0
Naupliar *"Paracalanus"*[1]	5,282	4,229	2,491	2,379	2,500	8,352	2,215	1,277	1,051	1,041	748
Naupliar *Calanus*	691	441	1,008	744	2,033	579	340	81	81	41	71
Naupliar *Rhincalanus*	0	72	0	8	8	97	23	0	0	0	0
Other nauplii	2,636	5,507	7,143	11,822	12,602	9,650	2,764	3,333	2,358	2,073	1,594
Female *Acartia*	14	8	25	59	52	16	0	0	0	0	0
Male *Acartia*	21	0	25	16	21	4	0	0	0	0	0
Copepodite *Acartia*	45	47	517	1,784	2,546	83	72	4	0	0	0
Adult *Labidocera*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Labidocera*	532	98	75	80	0	0	0	0	0	0	0
Adult and copepodite *"Paracalanus"*[1]	3,040	2,047	2,264	2,066	2,033	6,364	3,574	3,191	2,412	1,165	435
Appendicularians	2,535	2,907	3,218	4,164	6,134	1,736	488	255	45	37	7
Adult and copepodite *Oithona*	282	157	1,345	2,231	3,821	1,992	1,824	1,404	545	805	725
Adult and copepodite *Euterpina*	67	36	130	2,320	1,736	413	130	0	0	0	0
Euphausiid nauplii	0	0	4	33	4	17	0	8	4	0	0
Euphausiid calyptopis	14	13	4	40	46	21	0	4	0	4	7
Euphausiid furcilia	8	4	4	24	25	19	47	26	33	73	7
Chaetognaths	45	141	189	252	142	93	85	41	28	22	11
Female *Calanus*	0	0	0	4	16	4	0	0	0	0	0
Male *Calanus*	0	0	0	0	0	0	0	0	0	0	0
C V *Calanus*	0	11	17	15	21	4	0	4	0	0	0
C IV *Calanus*	14	14	17	19	10	4	4	0	4	0	4
C III *Calanus*	0	0	4	0	16	50	10	0	0	0	0
C II *Calanus*	0	0	0	12	21	161	20	0	0	0	0
C I *Calanus*	0	4	13	4	49	119	9	0	0	0	0
Adult *Corycaeus*	14	16	91	123	142	194	163	119	70	61	36
Adult and copepodite *Oncaea*	240	157	0	0	325	3,636	3,453	1,707	1,284	1,487	1,143
Microsetella	141	394	613	1,440	1,220	579	488	71	19	33	36
Adult *Metridia*	0	0	0	0	0	4	0	20	33	15	7
Adult *Pleuromamma*	0	0	0	4	0	11	23	45	28	26	18
Copepodite *Metridia* and *Pleuromamma*	4	0	4	45	29	153	293	203	167	134	112
Adult *Rhincalanus*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Rhincalanus*	0	0	8	7	10	23	51	33	4	0	0
Copepodite *Eucalanus*	0	0	0	0	0	12	8	8	0	0	0
Other copepods	4	4	0	0	0	0	0	8	12	23	24
Fish eggs	4	0	0	0	3	0	0	0	0	0	0
Fish larvae	21	7	67	59	28	11	8	0	0	0	0
Cladocerans (*Evadne*)	120	101	13	4	0	4	0	0	0	0	0
Polychaete larvae	14	22	50	96	366	257	169	80	12	31	32
Lamellibranch larvae	0	0	0	0	0	0	0	0	0	0	0
Cyphonautes larvae	0	0	0	20	8	4	0	0	0	0	0
CHLOROPHYLL	median micrograms per liter										
	0.24	0.29	0.49	0.68	0.85	1.82	1.42	0.97	0.51	0.32	0.26
PHYTOPLANKTON + CILIATES	median number per 100 ml										
Nitzschia spp. S	1,036	2,181	791	372	1,593	162	841	241	217		
Bacteriastrum spp. (chains)	36	90	44	78	14	168	108	50	18		
Chaetoceros spp.	5,974	1,855	3,628	2,008	1,814	3,585	2,035	1,428	435		
Rhizosolenia alata	88	122	96	72	34	28	6	2	4		
Rhizosolenia fragilissima	108	160	114	70	68	11	8	2	4		
Skeletonema costatum	56	74	70	8	10	18	96	52	116		
Ceratium spp.	18	24	38	32	18	28	4	2	0		
Gonyaulax polyedra polygramma	10	2	54	26	18	2	0	0	0		
Prorocentrum sp. C	2	0	58	76	50	6	0	0	0		
Protoperidinium spp.	14	16	12	22	23	32	10	0	0		
Cochlodinium catenatum	46	96	456	1,092	1,869	2,064	522	68	0		
Gymnodinium splendens	0	0	2	12	241	21	0	0	0		
Torodinium robustum	28	30	12	12	7	0	0	0	2		
Umbilicosphaera sibogae	16	0	16	86	0	30	2	2	0		
Emiliania huxleyi	858	1,518	1,498	706	1,372	2,173	3,009	1,580	957		
Mesodinium rubrum	2	34	6	4	0	11	4	6	4		
Laboea spp.	102	74	134	122	217	125	44	24	14		
Lohmaniella spp.	210	84	152	174	118	123	30	20	12		

[1]Includes some *Clausocalanus*.

APPENDIX TABLE 4.—Nocturnal profiles after storm.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON	median number per cubic meter										
Naupliar *Acartia*	6,590	9,360	17,323	18,008	15,106	11,371	660	176	90	230	0
Naupliar *Labidocera*	1,172	1,181	394	336	0	0	0	0	0	0	0
Naupliar *"Paracalanus"*[1]	4,908	5,256	7,591	4,370	5,184	9,091	6,400	3,424	1,345	1,073	1,126
Naupliar *Calanus*	1,099	1,378	1,969	1,533	1,082	1,489	495	467	545	236	260
Naupliar *Rhincalanus*	0	0	0	0	0	167	7	4	0	0	0
Other nauplii	3,678	7,102	12,795	27,969	11,873	12,553	8,000	6,154	5,364	4,245	3,520
Female *Acartia*	11	23	66	138	13	0	0	0	0	0	0
Male *Acartia*	11	28	17	123	27	0	0	0	0	0	0
Copepodite *Acartia*	280	661	1,575	2,299	1,505	3,617	32	0	0	0	0
Adult *Labidocera*	11	0	0	0	0	0	0	0	0	0	0
Copepodite *Labidocera*	119	80	31	15	0	0	0	0	0	0	0
Adult and copepodite *"Paracalanus"*[1]	4,215	3,977	2,953	2,490	1,915	4,013	5,400	2,731	1,887	720	1,039
Appendicularians	2,835	4,400	4,921	5,556	2,814	4,255	4,200	881	377	307	80
Adult and copepodite *Oithona*	172	394	495	347	1,003	1,505	1,800	952	755	169	560
Adult and copepodite *Euterpina*	57	142	110	1,261	3,617	167	165	16	27	5	0
Euphausiid nauplii	0	0	0	0	0	0	14	9	14	20	13
Euphausiid calyptopis	57	40	37	83	17	4	13	7	9	8	0
Euphausiid furcilia	11	0	29	61	27	13	11	26	9	16	9
Chaetognaths	95	100	202	215	54	112	49	57	9	19	9
Female *Calanus*	0	0	0	15	17	0	0	0	0	0	0
Male *Calanus*	0	0	0	0	0	0	4	0	0	0	4
C V *Calanus*	4	11	0	15	9	13	0	0	4	0	0
C IV *Calanus*	4	23	26	0	43	27	7	0	0	4	0
C III *Calanus*	7	31	26	31	34	80	13	0	0	0	0
C II *Calanus*	0	16	26	42	43	85	0	0	0	0	0
C I *Calanus*	7	16	8	0	0	68	7	0	0	0	0
Adult *Corycaeus*	11	0	47	252	732	190	130	55	45	28	14
Adult and copepodite *Oncaea*	230	240	94	1,513	1,003	2,766	4,400	1,868	1,345	1,792	1,200
Microsetella	115	320	495	347	426	334	660	78	245	46	20
Adult *Metridia*	0	8	16	0	0	13	7	4	9	5	0
Adult *Pleuromamma*	8	16	16	0	0	0	32	44	31	5	9
Copepodite *Metridia* and *Pleuromamma*	8	8	16	17	0	202	366	229	188	88	44
Adult *Rhincalanus*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Rhincalanus*	0	0	12	0	17	67	18	4	9	0	4
Copepodite *Eucalanus*	0	0	0	0	0	0	0	0	5	0	0
Other copepods	4	0	0	15	27	51	16	18	54	15	26
Fish eggs	0	16	4	0	0	0	0	0	0	0	0
Fish larvae	0	0	26	42	0	0	0	0	0	0	0
Cladocerans (*Evadne*)	29	197	330	17	0	0	0	0	0	0	4
Polychaete larvae	18	20	106	276	272	334	165	311	47	27	20
Lamellibranch larvae	0	0	0	0	0	0	0	0	0	0	0
Cyphonautes larvae	0	0	4	56	121	67	25	0	0	0	0
CHLOROPHYLL	median micrograms per liter										
	1.17	1.34	2.87	3.87	4.15	3.11	1.01	0.61	0.46	0.38	0.35
PHYTOPLANKTON + CILIATES	median number per 100 ml										
Nitzschia spp. S	88	0	0	88	0	0	0	43	130		
Bacteriastrum spp. (chains)	194	9	8	0	0	0	12	12	0		
Chaetoceros spp.	5,221	9,469	3,363	442	4,071	4,690	783	174	217		
Rhizosolenia alata	56	19	32	19	8	0	0	4	0		
Rhizosolenia fragilissima	83	0	0	111	0	0	4	20	0		
Skeletonema costatum	0	0	0	0	0	0	40	0	8		
Ceratium spp.	111	46	80	167	32	24	4	0	2		
Gonyaulax polyedra polygramma	0	28	40	37	41	0	0	0	0		
Prorocentrum sp. C	556	806	1,360	1,704	290	88	4	0	0		
Protoperidinium spp.	56	102	32	0	16	16	12	0	2		
Cochlodinium catenatum	1,833	1,519	1,488	3,259	3,343	3,424	516	56	10		
Gymnodinium splendens	306	352	464	370	4,102	1,016	32	0	0		
Torodinium robustum	56	37	64	74	16	40	4	0	0		
Umbilicosphaera sibogae	28	9	24	74	24	16	4	0	0		
Emiliania huxleyi	1,062	1,327	1,858	1,416	2,035	2,035	1,652	1,043	478		
Mesodinium rubrum	389	176	72	241	14	16	12	0	0		
Laboea spp.	472	222	344	389	97	400	72	36	8		
Lohmaniella spp.	528	435	512	1,185	207	552	180	24	4		

[1]Includes some *Clausocalanus*

DIEL AND DEPTH VARIATIONS IN THE SEX-SPECIFIC ABUNDANCE, SIZE COMPOSITION, AND FOOD HABITS OF QUEENFISH, *SERIPHUS POLITUS* (SCIAENIDAE)

EDWARD E. DEMARTINI,[1] LARRY G. ALLEN,[2] ROBERT K. FOUNTAIN,[1] AND DALE ROBERTS[1]

ABSTRACT

Lampara seine-hauls were taken during day and night over 5-27 m bottom depths off the coast of northern San Diego County, California, from September 1979 to March 1981. These samples were used to characterize the temporal and spatial patterns of the abundances and size and sex compositions of queenfish, *Seriphus politus*, in an unprotected, coastal environment. Stomach contents of sample queenfish were examined to aid our interpretation of these patterns.

Adult queenfish of both sexes made diel, onshore, and offshore migrations, but immature fish generally did not. Both immatures and adults occurred in epibenthic, resting schools in shallow areas (~10 m or less depth, within ~1.5 km of shore) during the day. At night, adult fish dispersed (to >3.5 km) offshore. On average, a greater fraction of the adult males emigrated farther offshore at night than adult females. Immature fish remained inshore of 16 m bottom depths (within ~2.5 km of shore) at night, with the majority staying inshore of ~10 m depth. Regardless of maturity class, larger fish occurred farther offshore at night.

Stomach contents data confirmed the primarily nocturnal feeding habits of both immature and adult queenfish. Immatures fed primarily on meroplankton and other nearshore prey; however, adults captured offshore had also eaten some nearshore prey. Thus, food habits explain much, but not all of the diel migratory pattern. Immature queenfish may also remain nearshore at night because migration is not worthwhile energetically and because of greater risk of predation offshore. Adults perhaps also migrate offshore at dusk to spawn.

Numerous physical and biological factors influence the spatial and temporal distribution patterns of fishes. In response to such factors, coastal marine fishes often undergo diel shifts in spatial distributions (reviewed by Woodhead 1966; Blaxter 1970). Examples of horizontal (Hobson 1965, 1973; Hobson and Chess 1976; Quinn et al. 1980; Allen and DeMartini 1983) and vertical or water-column (Parrish et al. 1964; Woodhead 1964; Beamish 1966) diel migrations are recognized. Diel horizontal migrations may vary with life stage (e.g., see Hobson and Chess 1973). The type of diel vertical movement also may vary with season and with age and spawning condition of fish (Hickling 1933; Lucas 1936; Brawn 1960; Blaxter and Parrish 1965; Beamish 1966). In other cases, relatively static differences between the depth distributions of juvenile and adult life stages have been documented (reviewed by Helfman 1978). Spatial segregation of adult males and females has been commonly observed only in tropical reef fishes (Moyer and Yogo 1982; Clavijo 1983; and others).

This study describes the manner in which a complex interplay of the factors listed above can determine the temporal and spatial patterns of the distribution of a temperate marine fish. Specifically, we report on diel shifts in the onshore, offshore distribution of queenfish, *Seriphus politus*, characterize the variation in these diel shifts for immature, adult male, and adult female fish, and relate these shifts to feeding, antipredator, and breeding functions previously described.

The queenfish is a small, schooling sciaenid whose center of geographic distribution lies in the Southern California Bight, south of Point Conception (Miller and Lea 1972). The species contributes significantly to the sport fish catch on piers in southern California (Frey 1971) and provides forage for several game fishes (Young 1963; Feder et al. 1974). Queenfish form inactive, epibenthic schools nearshore (at ~10 m or less bottom depth)

[1]Marine Science Institute, University of California, Santa Barbara, Calif.; present address: Marine Review Committee Research Center, 531 Encinitas Boulevard, Suite 114, Encinitas, CA 92024.

[2]Marine Science Institute, University of California, Santa Barbara, Calif.; present address: Department of Biology, California State University, Northridge, CA 91330.

Manuscript accepted March 1984.
FISHERY BULLETIN: VOL. 83, NO. 2, 1985.

during the day (Hobson and Chess 1976; Allen and DeMartini 1983). Queenfish are dispersed throughout the water column and also occur farther offshore (to 20-30 m depths) at night, where they feed (Hobson and Chess 1976; Hobson et al. 1981; Allen and DeMartini 1983) and perhaps spawn (DeMartini and Fountain 1981).

This study represents part of an ongoing environmental impact assessment of the fishes of coastal waters off San Onofre Nuclear Generating Station near Oceanside, Calif., using the queenfish as a target species. Recognition of potentially complex patterns of spatial and temporal distribution has general applicability for the design and interpretation of analogous monitoring studies and for other assessments of nearshore fish stocks (June 1972).

METHODS AND MATERIALS

Sampling Design

Catches made by lampara seines (a type of semipursing, roundhaul net, Scofield 1951) were used to characterize the distribution and abundance of queenfish in terms of catch per unit effort (CPUE), where a standard-area seine-haul was defined as the unit of effort (Allen and DeMartini 1983). All queenfish present in each seine-haul were counted aboard ship. Seines fished from sea surface to seabed over bottom depths from 5 to 27 m. For diel comparisons, a total of 14 pairs of "day" (1-6 h after sunrise) and "night" (1-6 h after sunset) cruises were made during the period from September 1979 to March 1981, inclusive. On each cruise, 1 or 2 seine-hauls were made within randomly selected subareas within each of three depth blocks (shallow, 5-10 m, 0.5-1.5 km offshore; middepth, 11-16 m, 1.5-2.5 km offshore; deep, 18-27 m, 2.5-3.5 km offshore) at each of two longshore locations, about 5 and 22 km upcoast of Oceanside, Calif. Two replicate hauls were made at each longshore location in the shallow depth block (wherein catches were most variable) on day cruises, and the two catch values averaged. For a chart of the study area and further details of gear and sampling designs, see Allen and DeMartini (1983).

CPUE and Size-Composition Data

A maximum of two subsamples of ~50 individuals each of queenfish of all sizes were randomly selected from each seine-haul and placed on ice aboard ship. In the laboratory, all fish in the subsamples were sexed macroscopically (DeMartini and Fountain 1981) into immatures (of both sexes), adult males, adult females, and sex indeterminable. (Fish of indeterminable sex comprised <5% of total catch.) Fish were measured to the nearest millimeter standard length (SL) and grouped into 5 mm length classes for analysis. For seine-hauls in which the total number of queenfish caught exceeded the total number measured, the numbers of fish of each maturity and sex category caught were estimated from the respective number measured, standardized to the total number of queenfish caught. In these cases, the length frequencies of the fishes in each sex category measured were then weighted by the estimated number of that category present in the haul.

Queenfish length-frequency data were compared between diel periods and depth blocks by Kolmogorov-Smirnov Two-Sample test (Siegel 1956). A nonparametric 3-way ANOVA (Wilson 1956), available in the IMSL Library's[3] statistical package, was used to simultaneously evaluate the effects of diel period, depth block, sampling date (cruise), and their potential interactions on the numerical CPUE of immature, adult male, and adult female fish. In all ANOVA analyses, catches made within the same depth block at the two longshore locations on a given cruise were considered separate estimates, as differences between locations were sometimes evident.

Food Habits

Additional subsamples of one queenfish per 10 mm SL length class were randomly selected from seine-hauls for analysis of food habits. Fish were examined from a larger series of 11 day and 23 night cruises (that included 8 of the aforementioned 14 paired, day/night cruises) conducted during September 1979-October 1980. These subsampled fish were placed in 10% Formalin[4] immediately following capture, after their abdominal walls had been slit to accelerate preservation. Stomachs were dissected and placed in 70% ethyl alcohol after about 1 wk of fixation. Contents of stomachs were scored for state of digestion on a scale of 0 (undigested) to 10 (prey present but totally indistinguishable). All prey were identified to lowest taxonomic category, their numbers tal-

[3]IMSL Library, Sixth Floor, NBC Building, 7500 Bellaire Blvd., Houston, TX 77036.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

lied, and reconstructed wet weight biomass estimated (to the nearest milligram, based on a key of reference prey weights). Values were summed for the aggregate of each taxon in each stomach. A compound measure of numbers (N), weight (Wt), and frequency occurrence (FO) of prey (IRI = {(%N + % Wt)%FO}; Pinkas et al. 1971) was used to characterize temporal and spatial variations in the overall importance of various prey to the diet of immature and adult male and female queenfish.

RESULTS

Catch per Unit of Effort

A large majority of the adults of both sexes, as well as immature queenfish, occurred at shallow depths (5-10 m) during daylight hours throughout most of the year (Fig. 1). A plurality of immature and adult fish of both sexes occurred at shallow depths at night as well; however, the distribution of numbers spread farther offshore at night, especially for adult fish (Fig. 1). The nocturnal offshore distribution appears to have been especially marked for adult males (Fig. 1B). This diel shift in the depth distribution of queenfish is characterized by the diel-by-depth interaction term in the ANOVA (Table 1). The (nearly) significant date effect for adults (and insignificant date effect for immatures) in the ANOVA (Table 1) reflects the general offshore emigration of adult, but not immature, queenfish during late fall and early

TABLE 1.—Results of Wilson's Three-Way Nonparametric ANOVA with equal replication (Wilson 1956) for the effects of diel period (day, night), bottom depth (5-10, 11-16, 18-27 m), and date (cruise) on the lampara seine CPUE of immature, adult male, and adult female queenfish. Data for 14 paired, day/night cruises made during the period from September 1979 to March 1981, inclusive. (* denotes significance at $P \leq 0.05$).

Maturity/ sex category	Factor	χ^2	df	P
Immatures	Diel	27.5	1	<0.001*
	Depth	52.0	2	<0.001*
	Date	10.0	13	0.69
	Diel x Depth	9.3	2	0.01*
	Diel x Date	7.8	13	0.86
	Depth x Date	14.0	26	0.97
	D x D x D	11.3	26	0.99
Adult males	Diel	34.4	1	<0.001*
	Depth	38.9	2	<0.001*
	Date	19.9	13	0.10
	Diel x Depth	5.2	2	0.08
	Diel x Date	5.6	13	0.96
	Depth x Date	13.1	26	0.98
	D x D x D	14.8	26	0.96
Adult females	Diel	50.6	1	<0.001*
	Depth	16.1	2	<0.001*
	Date	30.0	13	0.005*
	Diel x Depth	14.0	2	0.001*
	Diel x Date	7.0	13	0.90
	Depth x Date	11.4	26	0.99
	D x D x D	10.8	26	1.00

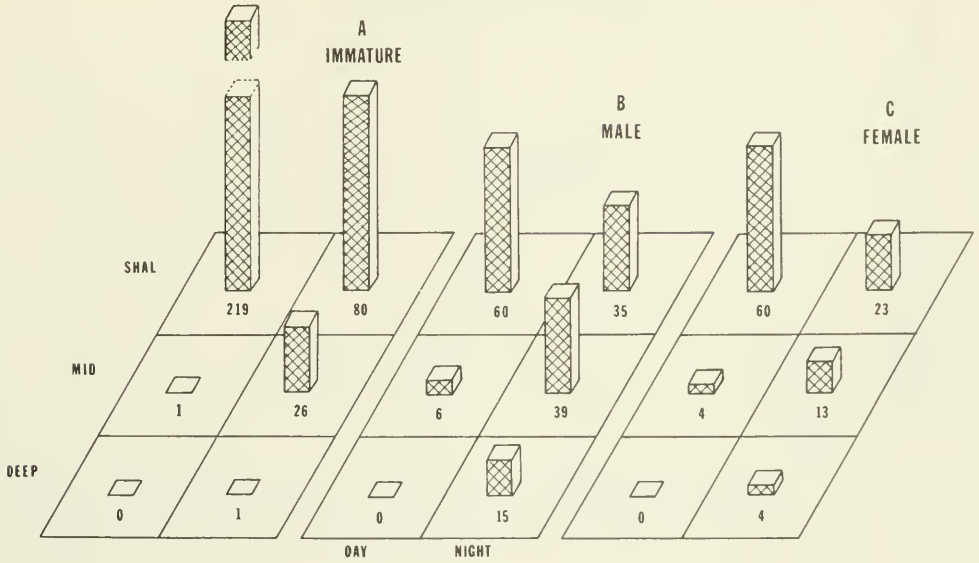


FIGURE 1.—Bar histogram chart of arithmetic mean CPUE (catch per seine haul) during the day versus at night, in the shallow (SHAL, 5-10 m), middepth (MID, 11-16 m), and deep (DEEP, 18-27 m) depth blocks, for immature, adult male, and adult female queenfish. All data represent samples from 14 paired, day/night cruises made from September 1979 to March 1981, inclusive.

winter (also see Allen and DeMartini 1983). The patterns illustrated by Figure 1 remained consistent throughout most of the year, when queenfish occurred nearshore (also see below).

Size Composition

The size composition of queenfish within sex and maturity classes also generally differed between diel periods within depth blocks (Fig. 2, Table 2). Adult males, adult females, and immature fish of both sexes were of generally larger body sizes in day versus night samples within the shallow depth block (Fig. 2, Table 2). At night, larger sized queenfish of all categories occurred in samples from middepths versus the shallow region (Fig. 3, Table 2).

The diel differences in the size composition of queenfish within depth blocks generally disappeared when catches were pooled over depth blocks throughout the year (Fig. 4). Specifically, the length-frequency distribution of each sex category in day-shallow samples closely resembled the size distribution of the respective category caught at night at 5-27 m depths (Fig. 4A, B, C), even though the large numbers of fish measured (hence great power) yielded statistically significant differences (Table 2). Clearly, queenfish present at 5-27 m depths at night occur at 5-10

TABLE 2.—Results of Kolmogorov-Smirnov Two Sample comparisons (Siegel 1956) of the length-frequency distributions of sample queenfish of various sex and maturity classes between diel periods and/or depth blocks. Based on all 14 D/N pairs of cruise data for the period September 1979-March 1981. See Figures 2-4 for data histograms.

Comparison	Dmax	D_{crit} 0.05	Significance level
Day vs. night, shallow depths			
Immatures	0.10	0.03	$P < 0.001$
Adult males	0.28	0.05	$P < 0.001$
Adult females	0.22	0.06	$P < 0.001$
Shallow vs. mid-depths, at night			
Immatures	0.26	0.06	$P < 0.001$
Adult males	0.24	0.06	$P < 0.001$
Adult females	0.12	0.09	$0.01 > P > 0.001$
Day-shallow vs. night-all depths			
Immatures	0.03	0.03	$P < 0.05$
Adult males	0.11	0.03	$P < 0.001$
Adult females	0.14	0.04	$P < 0.001$

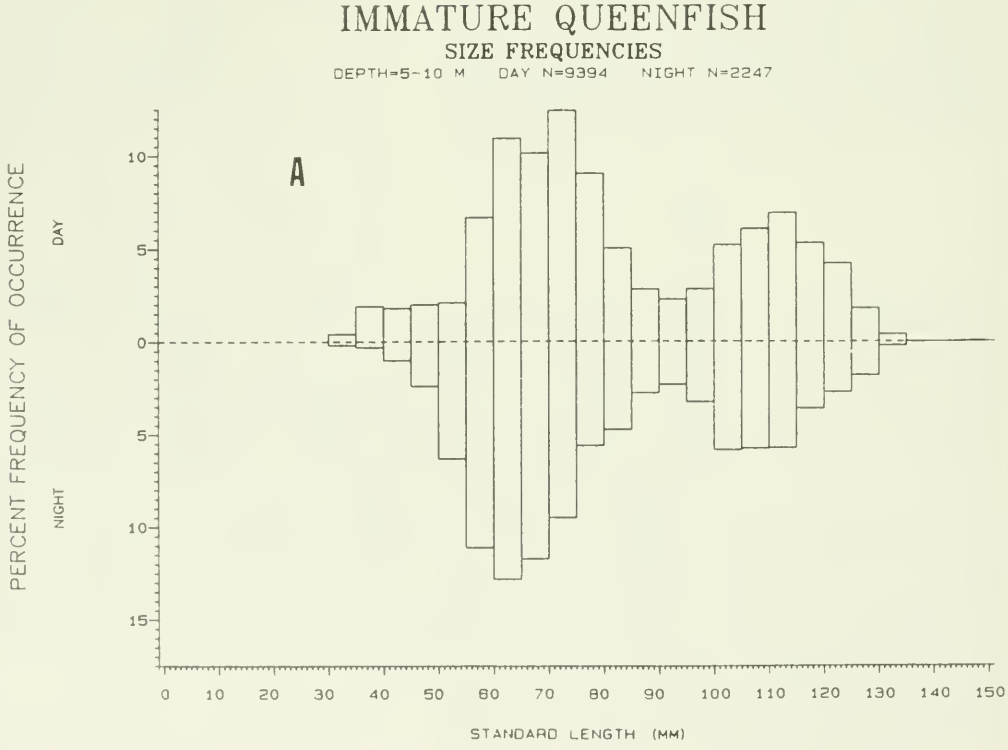
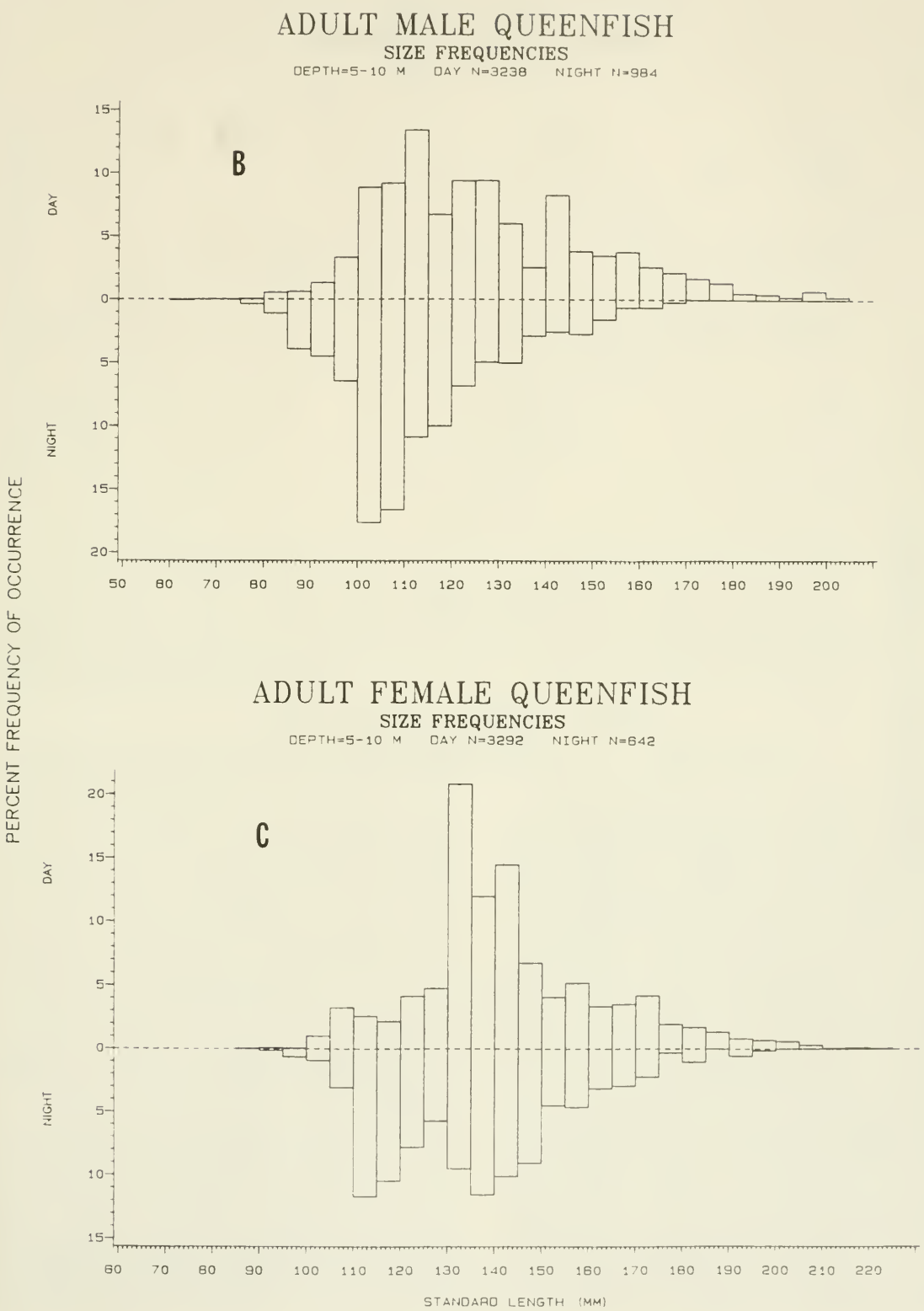
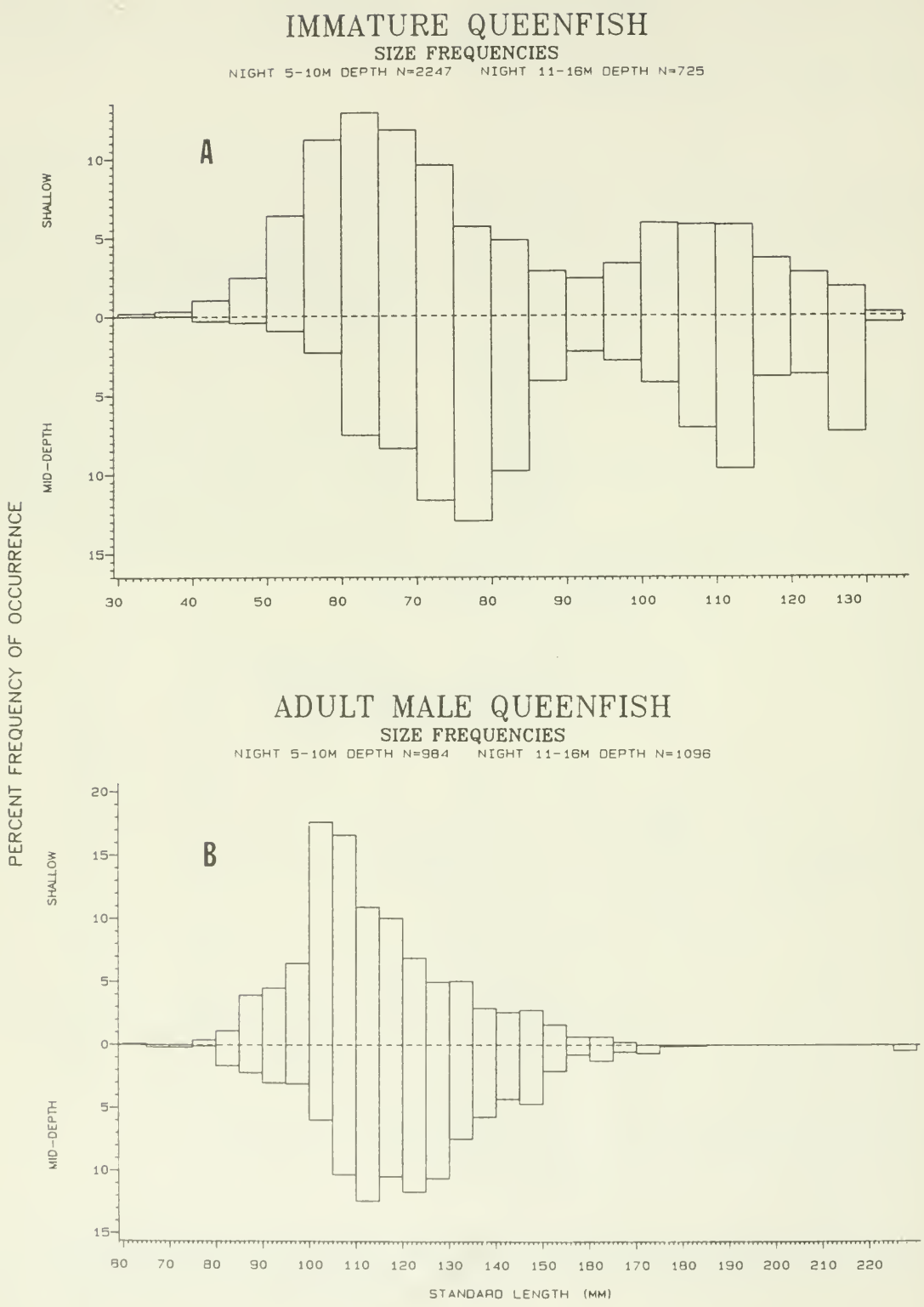


FIGURE 2.—Relative (percent) length-frequency distributions of (A) immature, (B) adult male, and (C) adult female queenfish, caught during the day versus at night in the shallow depth block (see Figure 1 caption for details). Day/night data are plotted above, below the horizontal axis in each panel.


ADULT MALE QUEENFISH
SIZE FREQUENCIES
DEPTH=5-10 M DAY N=3238 NIGHT N=984
B
DAY
NIGHT
15
10
5
0
5
10
15
20
50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200
ADULT FEMALE QUEENFISH
SIZE FREQUENCIES
DEPTH=5-10 M DAY N=3292 NIGHT N=642
C
DAY
NIGHT
20
15
10
5
0
5
10
15
60 70 80 90 100 110 120 130 140 150 160 170 180 190 200 210 220
STANDARD LENGTH (MM)
PERCENT FREQUENCY OF OCCURRENCE


IMMATURE QUEENFISH
SIZE FREQUENCIES
NIGHT 5-10M DEPTH N=2247 NIGHT 11-16M DEPTH N=725
A
SHALLOW
MID-DEPTH
10
5
0
5
10
15
30
40
50
60
70
80
90
100
110
120
130
ADULT MALE QUEENFISH
SIZE FREQUENCIES
NIGHT 5-10M DEPTH N=984 NIGHT 11-16M DEPTH N=1096
B
SHALLOW
MID-DEPTH
20
15
10
5
0
5
10
15
60
70
80
90
100
110
120
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140
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160
170
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190
200
210
220
STANDARD LENGTH (MM)
PERCENT FREQUENCY OF OCCURRENCE

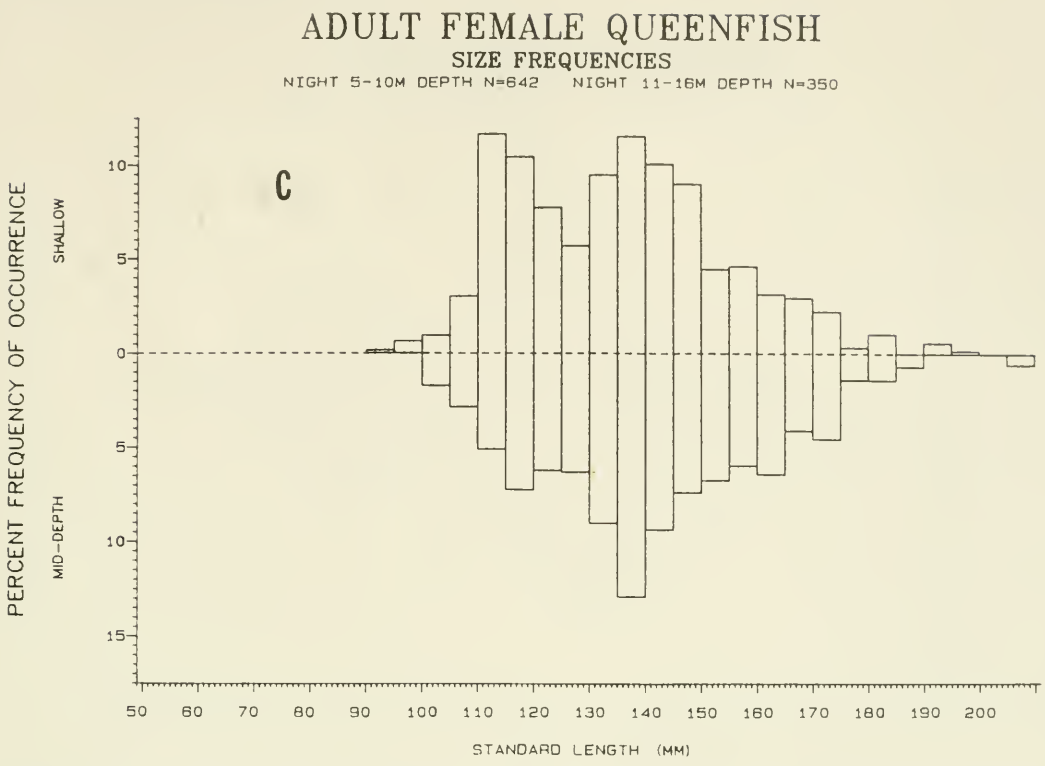


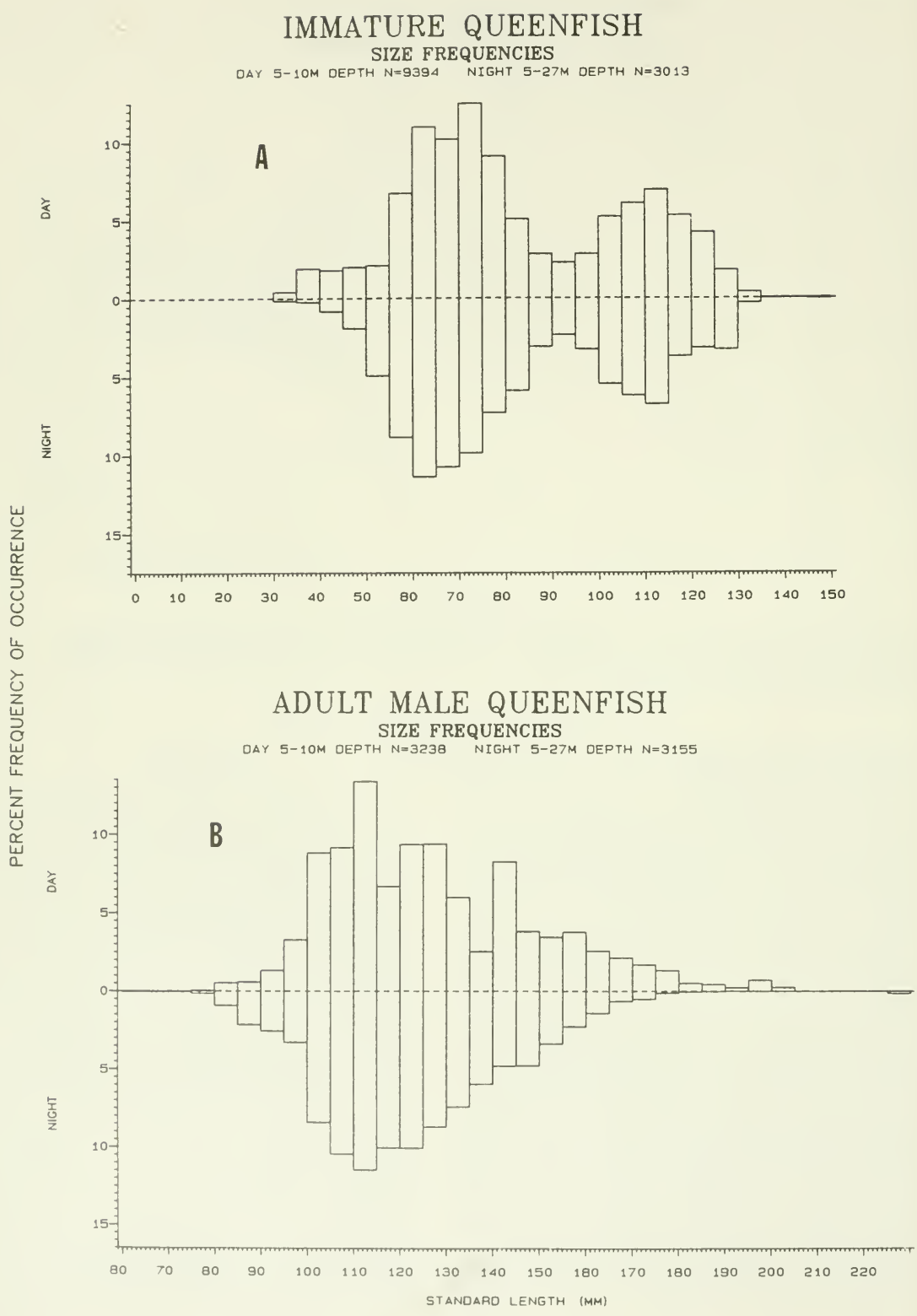
FIGURE 3.—Relative length-frequency distributions of (A) immature, (B) adult male, and (C) adult female queenfish caught during the night in the shallow versus middepth blocks (see Figure 1 caption for details). (Data for the deep depth block were too few to evaluate independently.)

m depths nearshore during the day (also see Discussion and Conclusions).

In order to further aid our interpretation of the function of the observed nocturnal offshore movements, we subdivided our diel catch data into three periods of year: 1) February-July (the onshore, breeding season; see DeMartini and Fountain 1981); 2) August-October (the onshore, nonbreeding season); and 3) November-January (the offshore, nonbreeding season). Analyses were restricted to size-frequency data for queenfish seined at shallow and middepths during the two periods of onshore distribution, as scant data on the size composition of adults were available for the offshore season. During both breeding and nonbreeding onshore periods, queenfish seined at shallow depths were larger during the day versus at night, and fish caught at night were consistently larger in middepth versus shallow collections (Table 3). Thus the year-round patterns illustrated by Figures 2 and 3 also basically characterize both breeding and nonbreeding periods of onshore distribution.

Food Habits

The food habits of immature, adult male, and adult female queenfish were evaluated for day and night collections made in the shallow- and middepth blocks during the onshore, breeding and onshore, nonbreeding periods of year. (Stomachs of fish from the deep depth block were not examined.) The purpose of these comparisons was to help interpret the relative importance of the feeding and breeding functions of diel offshore movements. We hypothesized that immature fish might remain onshore at night to feed on meroplanktonic (nocturnally active) demersal crustaceans and other prey more abundant at shallow depths. We further expected that adults emigrated offshore to spawn (DeMartini and Fountain 1981) and thereafter fed on relatimely larger prey that were more prevalent farther offshore. In general, immature queenfish fed on smaller prey than adult males, and adult males, being smaller than adult females, fed on generally smaller prey than females (Table 4). Contrary to expectations, adult


IMMATURE QUEENFISH
SIZE FREQUENCIES
DAY 5-10M DEPTH N=9394 NIGHT 5-27M DEPTH N=3013
A
DAY
NIGHT
10
5
0
5
10
15
0 10 20 30 40 50 80 70 80 90 100 110 120 130 140 150
ADULT MALE QUEENFISH
SIZE FREQUENCIES
DAY 5-10M DEPTH N=3238 NIGHT 5-27M DEPTH N=3155
B
DAY
NIGHT
10
5
0
5
10
15
80 70 80 90 100 110 120 130 140 150 180 170 180 190 200 210 220
STANDARD LENGTH (MM)
PERCENT FREQUENCY OF OCCURRENCE

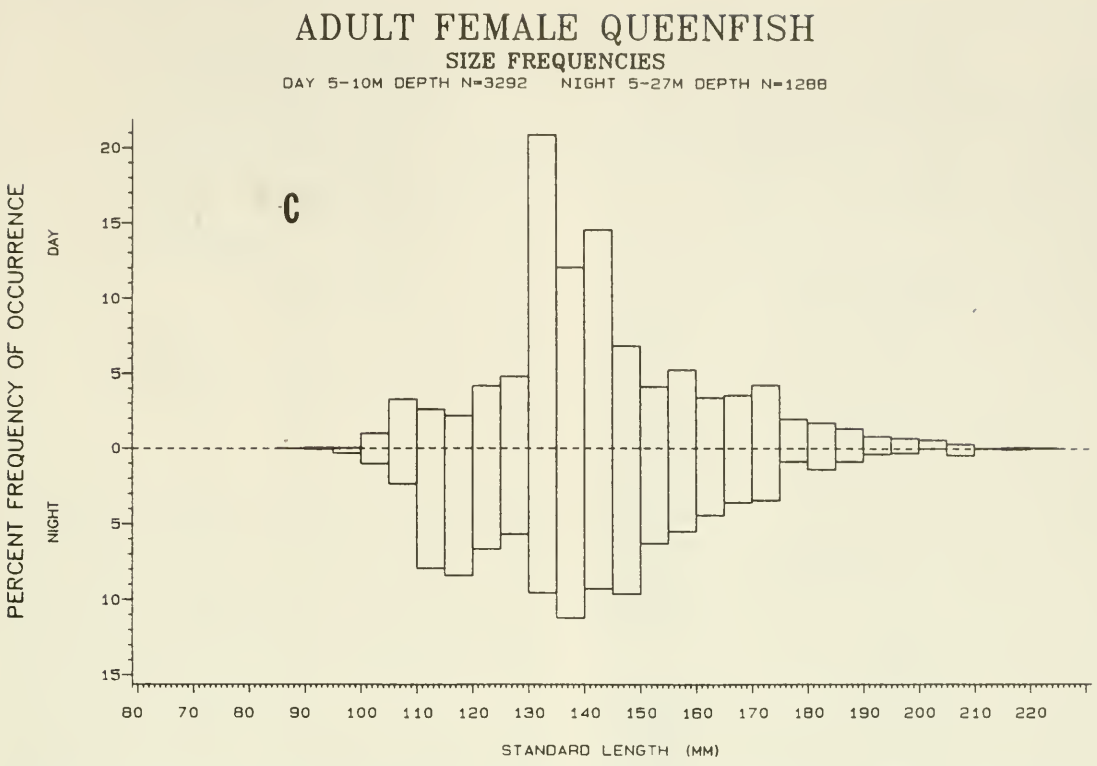


FIGURE 4.—Relative length-frequency distributions of (A) immature, (B) adult male, and (C) adult female queenfish caught during the day in the shallow depth block versus during the night in all depth blocks pooled (see Figure 1 caption for details).

TABLE 3.—Results of Kolmogorov-Smirnov Two Sample comparisons of the diel- and depth-specific length-frequency distributions of queenfish caught during the onshore, breeding versus onshore, nonbreeding periods of year. Qualitative results of comparisons are noted.

	Breeding			Nonbreeding		
	D > N?	Dmax	*P*	D > N?	Dmax	*P*
Day vs. night, shallow depths						
Immatures	yes	0.37	<0.001	yes	0.10	<0.001
Adult males	yes	0.06	0.05	yes	0.10	0.05 > *P* > 0.01
Adult females	yes	0.28	<0.001	yes	0.25	<0.001
	Mid > Shal?	Dmax	*P*	Mid > Shal?	Dmax	*P*
Shallow vs. mid-depths, at night						
Immatures	yes	0.19	<0.001	yes	0.33	<0.001
Adult males	yes	0.32	<0.001	yes	0.12	0.05
Adult females	yes	0.15	0.01	no	0.14	>0.1

queenfish of both sexes, as well as immatures, fed to large extents on prey (Table 4) whose centers of abundance were shallow (see Discussion and Conclusions). For immatures such major prey included holoplankton (*Labidocera trispinosa*) and meroplanktonic cumaceans (primarily *Diastylopsis tenuis*) (Table 4). *Diastylopsis tenuis* and other nearshore crustaceans also comprised nontrivial fractions of the diet of adult queenfish during the periods of onshore depth distribution (Table 4). *Diastylopsis tenuis*, a night-active meroplankter characteristic of the shallow region (see below), also occurred in the stomachs of fish collected at shallow depths during the day and during the night at middepths. Hence we feel justified to characterize the queenfish diet using data for both diel periods and depth blocks pooled in Table 4. State of prey digestion, though, tended to be less at

TABLE 4.—Prey taxa comprising ≥1% of the diet (by IRI) of immature, adult male, and adult female queenfish during the two periods of onshore distribution combined. Sample fish collected during both day and night and at shallow (5-10 m) and middepths (11-16 m) are pooled (see text). Diet characterized by number (*N*), reconstructed wet weight (Wt), and frequency of occurrence (FO) of prey; overall contribution to diet evaluated by IRI (Pinkas et al. 1971). Prey ranked by IRI within queenfish categories. *N* = number of fish examined that had food in their stomachs. Mean (and range) of body lengths (SL, mm) of fish examined were immatures—70 (34-100), adult males—127 (76-210), and adult females—146 (102-214).

	Type of prey	% IRI	% *N*	% Wt	% FO	Mean Wt/ prey (mg)
Immatures (*n* = 57)						
Labidocera trispinosa	holoplanktonic copepod	35.8	26.7	3.2	56.1	<0.2
Acartia tonsa	holoplanktonic copepod	20.9	40.2	2.8	22.8	<0.1
Metamysidopsis elongata	meroplanktonic mysid	15.6	5.9	7.9	52.6	1.7
Engraulis mordax	clupeoid fish	9.0	1.1	11.6	33.3	13.7
Diastylopsis tenuis	meroplanktonic cumacean	5.1	3.6	3.2	35.1	1.1
Ogyrides sp.	? meroplanktonic caridean shrimp	2.4	<0.1	31.9	3.5	472
Atylis tridens	meroplanktonic amphipod	2.1	2.0	2.6	21.1	1.7
Acanthomysis macropsis	meroplanktonic mysid	1.3	0.6	2.2	21.1	4.7
Blepharipoda occidentalis	? meroplanktonic megalops/juvs. (anomuran)	1.0	0.2	9.0	5.3	53.0
All other prey		6.8	19.6	25.6	—	1.7
Adult males (*n* = 228)						
Engraulis mordax	clupeoid fish	74.6	6.3	89.0	47.8	385
Diastylopsis tenuis	meroplanktonic cumacean	7.1	18.4	0.9	22.4	1.3
Metamysidopsis elongata	meroplanktonic mysid	6.4	10.0	0.8	36.4	2.1
Labidocera trispinosa	holoplanktonic copepod	6.4	14.9	0.1	25.9	<0.2
All other prey		5.5	50.4	9.2	—	5.0
Adult females (*n* = 236)						
Engraulis mordax	clupeoid fish	78.9	5.7	90.8	52.1	783
Metamysidopsis elongata	meroplanktonic mysid	6.5	10.8	0.5	36.4	2.3
Diastylopsis tenuis	meroplanktonic cumacean	3.7	10.8	0.3	21.2	1.2
Labidocera trispinosa	holoplanktonic copepod	3.1	10.2	<0.1	19.4	<0.2
Acanthomysis sculpta	meroplanktonic mysid	1.4	6.1	0.5	13.6	3.6
Caridean shrimp	? meroplanktonic	1.0	3.4	0.6	15.7	8.7
All other prey		5.4	53.0	7.3	—	6.9

night for both immature and adult queenfish (Table 5), indicating that all sizes of fish fed primarily at night.

DISCUSSION AND CONCLUSIONS

Functions of Nocturnal Offshore Dispersal in Queenfish

Diel migrations of queenfish have been previously reported. Queenfish have been directly observed emigrating offshore at dusk from inactive daytime schools nearshore at Santa Catalina Island, one of the Channel Islands offshore of the southern California mainland (Hobson and Chess 1976; Hobson et al. 1981). Similar behavior has been noted by Hobson[5] in mainland waters off La Jolla, near San Diego. Allen and DeMartini (1983) have characterized the general pattern of nocturnal offshore dispersal of queenfish near San Diego. Direct observation (Hobson and Chess 1976; Hobson et al. 1981) and examination of stomachs of fish collected during the day and at night (Hobson and Chess 1976; Hobson et al. 1981; Allen and DeMartini 1983; this study) confirm the primarily nocturnal feeding habits of queenfish. A spawning function has also been implicated for the offshore movements of adult queenfish at dusk (DeMartini

[5]Edmund S. Hobson, Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920, pers. commun. May 1978.

TABLE 5.—Results of Spearman's rank correlations (Siegel 1956) between index of state of digestion of stomach contents and time of collection for immature, adult male, and adult female queenfish. All samples collected prior to midnight. Sample fish collected during day, night, and at shallow (5-10 m) and middepths (11-16 m) are pooled over both onshore periods of distribution (see text).

	Digestion versus time		
	rho	*N*	*P*
Immatures	−0.35	57	0.007
Adult males	−0.20	228	0.003
Adult females	−0.22	236	<0.001

and Fountain 1981). During the February-July/August spawning season, ripe females with ovaries in hydrated (ready-to-spawn) condition can be collected throughout the daylight period beginning 1 h after sunrise, while females collected as soon as 1 h after sunset are either ripening (but nonhydrated) or are recently spent (DeMartini and Fountain 1981).

The diel distributional (CPUE) data of this study (Fig. 1) clearly illustrate the differences in diel migration made by immature, adult male, and adult female queenfish. Size-composition data (Figs. 2-4) further characterize the diel migrations as related to size of fish, regardless of maturity state or whether adults in the populations were reproductively active.

Certain aspects of the diel CPUE data suggest a breeding function for offshore dispersal at night, since only the distribution of immatures remained centered onshore at night. Also, a disproportionately greater number of adult males versus females emigrated offshore at night (Fig. 1B, C). This is consistent with an offshore migration by females for spawning that occurs on a less frequent than daily basis, since individual female queenfish ripen and spawn batches of eggs on average only once a week (DeMartini and Fountain 1981). The male-biased, daytime aggregations of ready-to-spawn queenfish (DeMartini and Fountain 1981) suggest that individual males spawn at more frequent than weekly intervals. Also, preflexion stages of queenfish larvae are most abundant in midwaters over 12-45 m bottom depths from 1.9 to 5.4 km offshore in the region of San Onofre-Oceanside (Barnett et al.[6]), which strongly suggests that most spawning occurs in outer nearshore regions.

Other distributional data, however, indicate a primarily feeding function for offshore dispersal at night. The nighttime, offshore shift in the distribution of adults of both sexes, for example, occurred during both the nonbreeding and breeding seasons. In addition, relatively more of the larger individuals among the immatures (as well as more of the larger adults of both sexes) moved offshore at night (Fig. 3) from the shallow region wherein queenfish of all sizes co-occurred during the day (Figs. 1, 4). The latter pattern persisted during both breeding and nonbreeding periods of year when distributions were generally inshore of 30 m bottom depth. On balance, the size composition of immature and adult female queenfish censused at 5-27 m depths at night resembled the composition of those censused at 5-10 m depths during the day (Fig. 4A, C), indicating that few very large immatures or females move offshore of 27 m at night. This moreover confirms that the queenfish seined offshore at night had resided at 5-10 m depths during the day and not in a region (e.g., shallower or deeper) that we did not census. Analogous data for adult males (Figs. 1, 4B) indicate that this may not be true for the largest males. However, the pattern of larger individuals farther offshore persisted for males as well as immatures and females during the nonbreeding period.

The diel food habit data also are largely consistent with the hypothesis that queenfish disperse offshore at night to feed, despite several discrepancies. Certain prey are known to be much more abundant at either extreme of the queenfish depth distribution. The presence of shallow-living "marker" species such as *Diastylopsis tenuis* (Table 6) in the stomachs of queenfish collected offshore of the respective prey distribution likely reflects some feeding activity just prior to or during the dusk offshore emigration. The presence of some night-active meroplankton in stomachs of fish collected during the day probably represents the partial confounding of nighttime foraging by circumdiel gut residence times. We consider it unlikely that queenfish feed on prey such as *D. tenuis* during the day, as the nocturnal activity patterns of this and other species of demersal meroplankton

[6]Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. Long term average spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS cooling system. A study submitted to the Marine Review Committee of the California Coastal Commission, July 22, 1980. Unpubl. rep., 32 p. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

TABLE 6.—Prey taxa comprising ≥1% of the diet (by IRI) of immature, adult male, and adult female queenfish collected during the night from the mid-depth (11-16 m) block. Data for the two periods of onshore distribution are pooled; for further details of diet characterization see Table 4. Mean (and range) of body lengths (SL, mm) were immatures—71 (42-86), adult males—126 (83-183), and adult females—147 (103-207).

	Type of prey	% IRI	% *N*	% Wt	% FO	Mean Wt/ prey (mg)
Immatures (*n* = 14)						
Engraulis mordax	clupeoid fish	25.2	2.6	27.2	42.9	16.8
Metamysidopsis elongata	meroplanktonic mysid	23.3	7.3	9.3	71.4	2.1
Acartia tonsa	holoplanktonic copepod	16.4	55.0	3.2	14.3	<0.1
Labidocera trispinosa	holoplanktonic copepod	15.0	16.2	1.6	42.9	<0.2
Ampelisca brevisimulata	? demersal amphipod	3.8	1.3	12.2	14.3	15.0
Diastylopsis tenuis	meroplanktonic cumacean	3.5	3.3	2.9	28.6	1.4
Acanthomysis macropsis	meroplanktonic mysid	3.1	1.3	4.2	28.6	5.2
Ampelisca cristata	? demersal amphipod	2.8	1.6	18.2	7.1	18.0
Blepharipoda occidentalis	? meroplanktonic juveniles (anomuran)	1.8	0.3	12.4	7.1	61.2
Hemilamprops californica	meroplanktonic amphipod	1.6	2.3	0.6	28.6	0.4
All other prey		3.5	8.8	8.2	—	1.6
Adult males (*n* = 125)						
Engraulis mordax	clupeoid fish	82.4	11.0	95.5	53.6	463
Labidocera trispinosa	holoplanktonic copepod	5.8	20.8	<0.1	19.2	<0.2
Metamysidopsis elongata	meroplanktonic mysid	4.0	8.4	0.4	31.2	2.3
Diastylopsis tenuis	meroplanktonic cumacean	3.2	12.2	0.3	17.6	1.3
All other prey		4.6	47.6	3.8	—	4.2
Adult females (*n* = 89)						
Engraulis mordax	clupeoid fish	83.6	9.1	93.0	59.6	615
Metamysidopsis elongata	meroplanktonic mysid	6.5	15.6	0.7	29.2	2.6
Diastylopsis tenuis	meroplanktonic cumacean	2.5	11.6	0.2	15.7	1.2
Labidocera trispinosa	holoplanktonic copepod	1.8	7.3	<0.1	18.0	<0.2
Hemilamprops californica	meroplanktonic amphipod	1.0	8.1	<0.1	9.0	0.4
All other prey		4.6	48.3	6.0	—	7.5

are well recognized (Barnard and Given 1961; Hobson and Chess 1976).

The significant amount of shallow-living prey such as *D. tenuis* and *Labidocera trispinosa* present in the stomachs of queenfish captured offshore at night (Table 6) nonetheless clearly illustrates that these fish had recently emigrated from depths nearer to shore. Numerous data characterize *D. tenuis* as largely restricted to within the 30 m isobath (Barnard and Given 1961; Parr and Diener[7]). *Diastylopsis tenuis*, in fact, declines >1 order of magnitude in abundance in benthic core samples between 8 and 15 m depths near San Onofre (Parr and Diener footnote 7). *Labidocera trispinosa*, a holoplanktonic copepod, also has been described as much more abundant inshore of 12-15 m bottom depths, both off La Jolla (Barnett 1974) and off San Onofre-Oceanside (Barnett et al.[8]). It seems less likely that nearshore forms such as *D. tenuis* and *L. trispinosa* are more available as prey offshore at night, since they are markedly less abundant offshore.

The presence of offshore prey in the stomachs of adult queenfish collected offshore obviously reflects nocturnal foraging while in that region.

[7]Parr, T. D., and D. D. Diener. San Onofre sand bottom benthic studies, San Onofre Nuclear Generating Station (SONGS) Units 2 and 3, pre-operation monitoring results, Volume 2. A study submitted to the Marine Review Committee of the California Coastal Commission, May 8, 1981. Unpubl. rep., 109 p. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

[8]Barnett, A. M., A. E. Jahn, P. D. Sertic, and S. D. Watts. The ecology of plankton off San Onofre Nuclear Generating Station, Volume 11. A study submitted to the Marine Review Committee of the California Coastal Commission, April 30, 1981. Unpubl. rep., 105 p. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

Neomysis kadiakensis, a mysid more abundant at depths corresponding to those frequented by adult queenfish at night (Clutter 1967; Bernstein and Gleye[9]), was a nontrivial component of the diet of adult queenfish that ranked third by weight in both males and females (although <1% of the total IRI for each sex). None of the immature queenfish that we sampled, however, had eaten any *N. kadiakensis*, even its juvenile stages (which also occur offshore, Bernstein and Gleye footnote 9). Nearshore prey, such as *L. trispinosa* and the demersal meroplankter, *D. tenuis*, were generally more important by weight and frequency of occurrence, if not numbers, in the diet of immature versus adult queenfish (Table 4). The tendency for immatures to remain closer to shore than adults and to feed on meroplankton (that are more abundant in sheltered areas closer to shore) has been noted for many species of nocturnal zooplanktivorous fishes on tropical coral reefs (Hobson and Chess 1978).

Both immature and adult queenfish are concentrated nearshore during the day, probably in response to pressure from diurnal predators (Hobson 1978; Allen and DeMartini 1983). Several species of voracious carnivores including Pacific mackerel, *Scomber japonicus*; Pacific bonito, *Sarda chiliensis* (Allen and DeMartini 1983); and California halibut, *Paralichthys californicus*, of piscivore-size (Plummer et al. 1983) are less abundant nearshore in the San Onofre-Oceanside region. The California halibut is a known predator of queenfish (Frey 1971; Plummer et al. 1983). The kelp bass, *Paralabrax clathratus*, another species known to prey on queenfish (Young 1963; E. DeMartini[10]), is most abundant in and near beds of giant kelp, *Macrocystis pyrifera*, that occur at 10-15 m bottom depths in the region (Larson and DeMartini 1984).

Overall, our data indicate that the nocturnal offshore dispersal of adults and the less contagious distribution of immatures nearshore at night are primarily for feeding. Allen and DeMartini (1983) reviewed and discussed the possible advantages of dispersal for feeding in schooling, zooplanktivorous fishes. To these we add the possible benefit (for adult queenfish) of foraging in regions where *N. kadiakensis*, a species of large mysid, is more abundant. It is also likely that the rate at which individual queenfish encounter planktonic prey is enhanced by foraging in regions farther offshore, where longshore currents are, on average, stronger (Reitzel[11]).

The nighttime, nearshore distribution of small immature queenfish also may be due to either or both of the following factors. First, small queenfish are undoubtedly incapable of making as extensive diel migrations as adults because of body size limitations. Hence the nearshore daytime distribution of immatures, probably set primarily by the influence of diurnal predators offshore, might limit the offshore movements of immatures at night. Second, predation pressure from nocturnal predators located farther offshore could restrict immature queenfish to nearshore regions. Potential nocturnal predators of immature queenfish include California halibut (Allen 1982) and California scorpionfish, *Scorpaena guttata* (Hobson et al. 1981). The nocturnal habits of other potential predators (Pacific mackerel, Pacific bonito, and Pacific barracuda, *Sphyraena argentea*) of small, immature queenfish are unknown. Large (>70 mm SL, Fig. 3) immature queenfish move offshore to some extent at night, which is also consistent with offshore dispersal to feed on larger prey, since size of prey is strongly related to queenfish body size (Tables 4, 6). Offshore dispersal of large immatures is nonetheless consistent with relaxed predation pressure, since susceptibility to predation must be inversely proportional to body size.

Rigorous evaluation of offshore dispersal for spawning would require censuses of the onshore, offshore distribution of recent spawning products. However, we are at present unable to routinely distinguish queenfish eggs or yolk-sac larvae <2.2-2.3 mm long (~4 d old or less) (Watson[12]).

In summary, we conclude that, as might be expected, the distributional (including migration) patterns of queenfish have feeding, predator avoidance, and perhaps other functions such as breeding.

[9]Bernstein, B. B., and L. G. Gleye. The ecology of mysids in the San Onofre region. A study submitted to the Marine Review Committee of the California Coastal Commission, April 30, 1981. Unpubl. rep., 72 p. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

[10]E. DeMartini, Marine Science Institute, University of California, Santa Barbara, CA 93106. Unpubl. data.

[11]J. Reitzel. 1979. Physical/chemical oceanography. *In* Interim Report of the Marine Review Committee of the California Coastal Commission. Part II: Appendix of Technical Evidence in Support of the General Summary, March 12, 1979, p. 6-23. Unpubl. rep. Marine Review Committee Research Center, 531 Encinitas Boulevard, Suite 106, Encinitas, CA 92024.

[12]W. Watson, Marine Ecological Consultants of Southern California, Inc., 531 Encinitas Boulevard, Suite 110, Encinitas, CA 92024, pers. commun. May 1983.

Comparison With the Diel Migrations of Other Fishes

Numerous other temperate (see Hobson and Chess 1976; Hobson et al. 1981; Allen and DeMartini 1983) and tropical (reviewed in Helfman et al. 1982) fishes are known to make horizontal migrations at dusk and dawn away from and back to reefs and other shallow areas. Such migrations have been characterized as a form of commuting between daytime resting/sheltering and nighttime feeding areas (Hobson 1965, 1973). These behaviors are most widely recognized for tropical coral reef-based fishes that forage on night-active benthic invertebrates in surrounding sandflats and seagrass beds or on nocturnal meroplankton in the water column (Hobson 1965, 1973; Domm and Domm 1973; Helfman et al. 1982; and others). The diel migration of queenfish certainly suggests feeding as a major, if not principal function. Both predator avoidance and feeding are probably major determinants of the nearshore distribution of immature queenfish. Feeding is probably the principal reason for the crepuscular onshore, offshore migrations of adults. Offshore movement for spawning may be of secondary importance, but data are inconclusive.

With the exception of the relatively short-range (within-reef) migrations observed for some tropical wrasses (see Moyer and Yogo 1982 and others), we are unaware of any study of the diel migratory behavior of nearshore temperate or tropical fishes that has demonstrated a primary spawning function for the behavior. We do not now believe that spawning is a major reason for the nocturnal offshore movements of queenfish, although we still feel that spawning is partly involved. We strongly recommend that future studies of the diel migratory patterns of temperate and tropical fishes be watchful for possible spawning as well as feeding activity.

ACKNOWLEDGMENTS

We thank Art Barnett for graciously allowing us to cite some of his unpublished data and Jan Fox for typing the manuscript. An anonymous reviewer helped us recognize the relative strengths and weaknesses of our arguments. This paper is the result of research funded by the Marine Review Committee (MRC), Encinitas, Calif. The MRC does not necessarily accept the results, findings, or conclusions stated herein.

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REACTION OF DOLPHINS TO A SURVEY VESSEL: EFFECTS ON CENSUS DATA

ROGER P. HEWITT[1]

ABSTRACT

A field experiment is described in which a helicopter was used to observe the efficiency of shipboard line-transect sampling of dolphin populations in the eastern tropical Pacific Ocean. Nineteen dolphin schools were tracked; 13 of these were detected by observers aboard the ship and 5 of these reacted to the approach of the ship by altering the direction and/or the speed of their movement; however, only 1 school reacted prior to shipboard detection. The results suggest that dolphin schools only occasionally react to the approach of a survey vessel prior to their detection by shipboard observers and that the use of a monotonically decreasing detection function is adequate to minimize bias. Aerial and shipboard estimates of school size and species composition for six schools compared favorably.

The Marine Mammal Protection Act of 1972 prohibits the harvest of marine mammals and specifies that the Federal Government may issue permits for their take only under special circumstances. One such circumstance involves the incidental kill of dolphins associated with the yellowfin tuna fishery in the eastern tropical Pacific Ocean. Before issuing the permits, the government must first certify the viability of the affected dolphin populations. To meet this requirement, scientists at the Southwest Fisheries Center define stocks and monitor their population demography, reproductive output, and abundance.

The vital statistics are derived primarily from specimens obtained from the tuna fishery. However, to estimate abundance, surveys are conducted using ships and aircraft independently of the fishery. The surveys, using line-transect methods (Burnham et al. 1980), have yielded estimates of the density of dolphins in the eastern tropical Pacific Ocean (Holt and Powers 1982). A critical assumption in the application of the method is that the animals do not move, in reaction to the observer, prior to their detection. In practice, a detection function, which is relatively insensitive to nonrandom movement, is used to describe the probability of observing a school of dolphins given its position relative to the observer's transect. A field experiment.was designed with the following objective:

1) Test the assumption that the animals do not alter their movement in reaction to the approach of a survey vessel *prior* to shipboard detection.

During a survey the unit of observation is a school of dolphins. In addition, species composition and the number of individual animals in a school (school size) are estimated. Surveys routinely collect information to determine the precision of these estimates by recording independent observations of several observers; however, determining their accuracy is more difficult and attempted less often (Holt and Powers 1982). Six schools were closely approached and observed from both an aircraft and a ship with the following objective:

2) Compare shipboard and aerial estimates of school size and species composition.

Although not an absolute determination of accuracy, the comparison yielded estimates from two very different viewpoints (high-altitude plan view versus low-altitude profile view).

A similar experiment was conducted using the NOAA Ship *Surveyor* and a ship-supported helicopter in 1977 (Au and Perryman 1982). They observed the reaction of eight dolphin schools to the approach of a ship; all eight schools swam away from the projected trackline of the ship. Au and Perryman also suggested that, in some cases, avoidance began beyond the visual range of shipboard observers. The present study was intended to collect additional data under a wider variety of conditions.

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted April 1984.
FISHERY BULLETIN: VOL. 83, NO. 2, 1985.

METHODS

The experiment was designed to observe the efficiency of shipboard survey operations by using a helicopter to track dolphin schools before, during, and after shipboard detection. This approach was an enhancement of the design employed by Au and Perryman (1982) which focused only on the behavior of the dolphins. A simulated survey operation was included in the experiment for the following reasons:

1) It was not reasonable to assume that movement of a dolphin school and the probability of detecting it are unrelated (i.e., it may be easier to see a school in full flight than one at rest). Therefore, associated data on movement and shipboard detection were collected for each school.
2) It was necessary to separate random movement from directed movement toward or away from the survey vessel. To do so unambiguously, the ship could not be directed toward a school detected by the helicopter, but rather had to continue searching along a predetermined transect.

From the experience gained on the 1982 survey (Holt 1983), we expected 80% of the sighting cues to be within 3 nmi of the transect line and <5 nmi ahead of the vessel. Furthermore, the Au and Perryman observations on eight schools suggested that dolphins may react to a ship 6 nmi away. With these considerations and prior experience in mind, the following field procedure was employed.

The ship proceeded at 12 kn in a direction selected so as to minimize glare from the sea surface. Two observers maintained constant watch through 25 power binoculars, mounted on the port and starboard sides of the flying bridge (11 m above the water); search patterns extended from the bow to the beam of the ship on each side. Records were kept of searching effort and sighting details. With the exception of selecting the transect direction, these are the same methods employed during previous dolphin surveys (e.g., Holt and Powers 1982). The helicopter searched a distance of 8 to 12 nmi ahead of the ship and 2 nmi to either side of the transect line, at right angles to the direction of the ship's travel (Fig. 1). Search altitude was 1,200 ft and speed was 60 kn. When a school was sighted by the helicopter, shipboard radar tracking began. The observers on the flying bridge were not aware of a track in progress until its termination. Schools were tracked for about an hour's time until one of three events occurred: 1) the school passed abeam of the ship; 2) the school passed beyond the visual range of shipboard observers; or 3) the aerial observers lost sight of the school and had to terminate the track prematurely; in all of the latter cases the presence of the animals was obscured by deteriorating sea state.

During a track, the helicopter was positioned over the school at a minimum altitude of 1,200 ft (370 m); the radar range and bearing to the helicopter were determined from the approaching survey vessel about every 4 min (an interval sufficient to record the appropriate navigational data and still provide continuity in the track). A transponder, mounted on the aircraft, facilitated accurate radar measurements. In addition, OMEGA navigation positions were recorded from dual systems aboard the helicopter and the ship. As the track progressed, field notes were taken on visual observations of school behavior and associated birds and fish. The tracking altitude appeared to

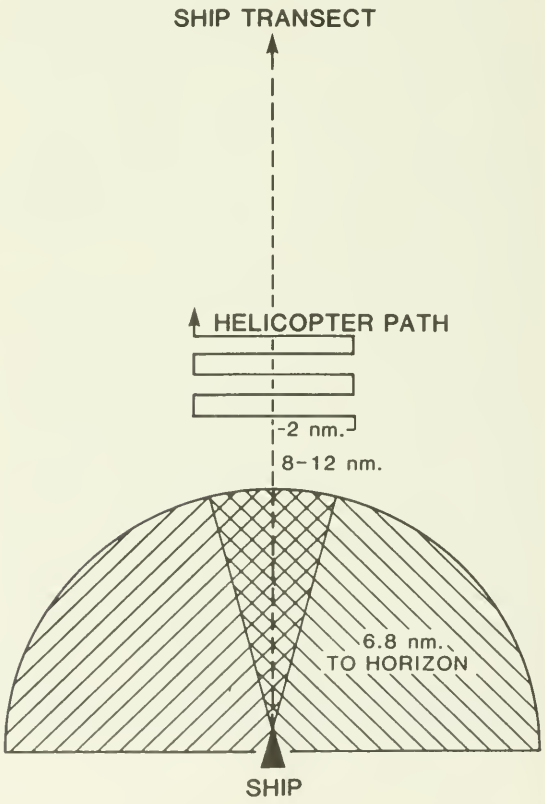


FIGURE 1.—Port and starboard search patterns (shaded areas) and path of helicopter (solid line) during transect (dashed line) surveys for dolphins.

be sufficient so as not to elicit a response from the animals. The dolphins appeared to be swimming calmly throughout the tracking; similar experience was reported by Au and Perryman (1982). It also placed the helicopter above the shipboard observers' vertical field of vision and therefore did not prematurely cue them on a school. Two oil drums were released and tracked at the beginning of the cruise to test the procedure: The resolution of radar measurements was 1-2° in bearing and 0.1 nmi in range; at 1,200 ft (370 m) altitude we were able to maintain visual contact with a 1 m object; and the shipboard observers were not aware of the helicopter until it was within 1 nmi of the ship, where the noise signaled its presence. Shipboard observers were questioned periodically throughout the experiment as to their cognizance of the helicopter; answers were always in the negative except when the binoculars were purposefully directed above the searching field. Observers were aware that looking for the helicopter would compromise the experiment and did not do so.

At the finish of a track, the helicopter descended to a lower altitude for additional photography and to estimate school size and species composition. The ship approached a limited number of schools to enable close-range shipboard estimates of the same school parameters. After school size and species composition were determined, normal survey operation resumed, with the helicopter searching ahead of the vessel and the shipboard observers actively scanning and recording search effort.

Relative motion radar plots were maintained. Apparent change in the relative direction of dolphin school movement was used as an indication of avoidance; field notes of aerial observations of behavior supplemented this information. The criteria defining reaction was a change of 30° or more in the direction of relative motion that was sustained over 2 or more subsequent fixes (Fig. 2).

The experimental design was opportunistic and only specifically designed to compare between a steam-powered survey vessel (NOAA Ship *Surveyor*) and a diesel-powered survey vessel (NOAA Ship *David Starr Jordan*). The experiment was conducted within a 100 square nmi area to the north and east of Clipperton Island (lat. 10°N, long. 110°W) during March and April 1983.[2] Observations were conducted with the *Surveyor* from 10 March through 17 March; the ship then ported at Manzanillo, Mexico, to take on fuel and subsequently met the *David Starr Jordan*, which had just completed a marine mammal survey[3] on 26 March at Clipperton Island. Observations were conducted in the same area with the *David Starr Jordan* until 7 April.

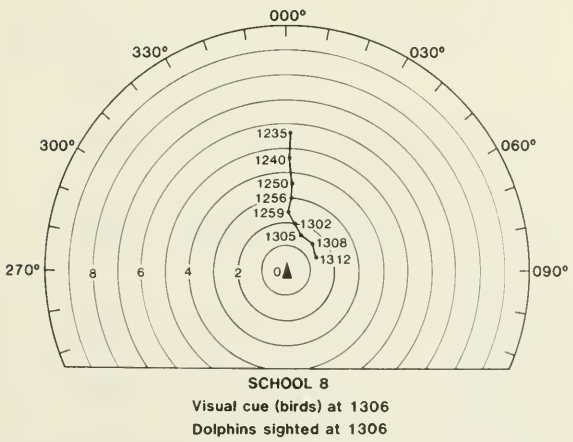
RESULTS

Avoidance

Tracks were started on a total of 26 dolphin schools, 5 in front of the *Surveyor* and 21 in front of

[2]Cruise Report NOAA Ship *Surveyor* Cruise RP-12-SU-83 dated May 24, 1983, on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[3]Cruise Report NOAA Ship *David Starr Jordan* Cruise DS-83-01 dated May 6, 1983, on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.



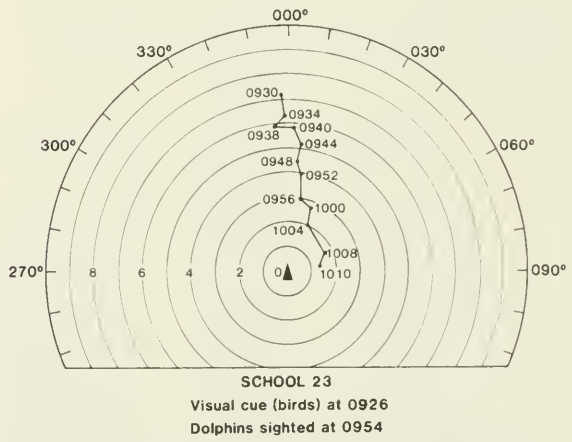


FIGURE 2.—Relative motion plots of dolphin school #8 and school #23. School #8 appeared to react to the approach of the ship; the sighting cue was reported after the dolphins' initial reaction. School #23 did not appear to react to the survey vessel.

the *David Starr Jordan;* a summary of the observations is listed in Table 1. Seven of the tracks were terminated prematurely, and of the remaining 19, 6 schools passed undetected by shipboard observers. These 6 schools did not appear to adjust their direction of movement in reaction to the survey vessel.

Of the 13 schools sighted by ship, 1 school altered its direction of movement in reaction to the approaching ship, prior to the detection of a sighting cue by the shipboard observers, and 12 schools did not appear to react before detection by the ship. One of the 12 schools was composed of rough toothed dolphins, *Steno bredanensis,* which are not a target of abundance surveys. Thus, from the results of this experiment, it is expected that 8% ($^1/_{12}$) of the target schools encountered on a survey will have moved (in reaction to the observer) prior to detection. This does not imply a corresponding degree of survey bias. Nonrandom movement, prior to detection, will alter the distribution of sighting distances and the detection function fit to the distribution; the survey will be biased to the extent that the functional form is sensitive to the data (see Discussion). Survey bias may also exist as a result of schools that react to the ship and are subsequently never seen by shipboard observers; if these schools would have been observed (the expectation is certain if they are on the transect line, less certain if they are off the line), then the bias is proportional to the fraction of schools that escaped detection. As stated above, no schools were observed to react to the ship and avoid detection.

The data suggest that dolphin schools may alter their direction of movement in reaction to the approach of a survey vessel. Thirty-eight percent ($^5/_{13}$) of the schools which were tracked by helicop-

TABLE 1.—Summary of dolphin school tracking data.

Vessel	School number	Beaufort sea state	Species composition		Number of individuals	Closest point of approach (nmi)	Reaction distance (nmi)	Radial sighting distance (nmi)	Relative bearing	Sighting cue	Interpolated radar position at time of sighting (range/bearing)
Surveyor	1	1	*Steno bredanensis*	100%	9	1.3	F[1]	2.5	317°	animals	1.8/335°
	2	1	*Stenella attenuata*	50%	175	7.0	F[1]	F[2]			
			S. longirostris	50%							
	3	3	*S. attenuata*	100%	53	2.5	F[1]	F[2]			
	4	5	Unidentified dolphins	100%	100	2.0	F[1]	2.0	030°	splashes	4.0/032°
	5	5	Unidentified dolphins	100%	15	F[3]					
Jordan	6	4	Unidentified dolphins	100%	22	F[3]					
	7	4	Unidentified dolphins	100%	35	F[3]					
	8	4	*S. attenuata*	25%	300	1.5	2.5	1.5	024°	birds	1.6/030°
			S. longirostris	5%							
			Unidentified dolphins	70%							
	9	4	Unidentified dolphins	100%	25	F[3]					
	10	4	*S. attenuata*	20%	150	0.5	1.7	6.0	003°	birds	6.3/002°
			S. longirostris	80%							
	11	4	*S. attenuata*	100%	25	5.0	F[1]	6.8[4]	023°	birds	7.2/019°
	12	4	*S. attenuata*	15%	65	7.0	F[1]	F[2]			
			S. longirostris	85%							
	13	4	*S. attenuata*	65%	175	1.3	2.2	6.8	356°	birds	6.2/357°
			S. longirostris	35%							
	14	4	*S. attenuata*	90%	50	2.5	F[1]	6.8[4]	000°	birds	8.1/354°
			S. longirostris	10%							
	15	4	*Stenella* spp.	100%	150	F[3]					
	16	4	*S. attenuata*	100%	35	1.2	1.5	6.0	357°	birds	7.0/359°
	17	3	Unidentified dolphins	100%	40	F[3]					
	18	3	*S. coeruleoalba*	100%	160	F[3]					
	19	3	*S. attenuata*	100%	45	3.0	F[1]	F[2]			
	20	0	*S. attenuata*	15%	260	1.7	F[1]	6.8[4]	355°	birds	6.7/353°
			S. longirostris	85%							
	21	2	*S. attenuata*	91%	230	6.4	F[1]	F[2]			
			S. longirostris	9%							
	22	1	*S. attenuata*	50%	180	2.1	2.1	6.8[4]	340°	birds	6.7/336°
			S. longirostris	50%							
	23	1	*S. attenuata*	50%	155	1.5	F[1]	6.8[4]	004°	birds	8.0/357°
			S. longirostris	50%							
	24	1	*S. coeruleoalba*	100%	29	0.1	F[1]	1.8	020°	animals	1.8/018°
	25	1	*S. attenuata*	40%	410	2.0	F[1]	4.0	015°	birds	5.0/010°
			S. longirostris	60%							
	26	1	*S. attenuata*	100%	85	3.0	F[1]	F[2]			

[1] School did not appear to react to the approach of the survey vessel.
[2] School passed undetected by shipboard observers.
[3] Track prematurely terminated.
[4] Cue observed on the horizon.

ter and detected by shipboard observers appeared to react to the ship. Spotted dolphins, *Stenella attenuata*, and spinner dolphin, *S. longirostris*, reacted at a distance of 0.5 to 2.5 nmi and were able to maintain a separation of 0.5 to 2.0 nmi from the ship; one school of striped dolphins, *S. coeruleoalba*, was successfully tracked and these animals stayed on a collision course with the ship until they were only a few hundred meters away. In all cases but one (school 8), the schools were detected by shipboard observers at distances far greater than the reaction distance.

None of the four dolphin schools successfully tracked in front of the *Surveyor* appeared to react to the approach of the ship. Five out of 15 schools appeared to react to the approach of the *David Starr Jordan*.

Estimates of School Size and Species Composition

Six schools were approached at close range by the *David Starr Jordan* so that shipboard observers could make estimates of school size and species composition using the same techniques that were used on previous abundance surveys. Estimates of school size and species composition were made independently by four to six shipboard observers and averaged, giving each an equal weight. These estimates compared favorably with estimates made by a single aerial observer stationed in the helicopter (Table 2). Shipboard estimates of school size ranged from 65 to 134% of the aerial estimates and averaged 101% (mean difference = 1.167; Pr = 0.713, paired t test of mean difference = 0); shipboard and aerial observers agreed on the species composition for all six schools compared, although there was some variation in the proportion assigned to each species.

DISCUSSION

The density estimator used in line-transect applications, formally derived by Burnham and Anderson (1976), and used to estimate the density of dolphin schools by Smith (1981) and Holt and Powers (1982), is:

$$\hat{D} = \frac{N\hat{f}(0)}{2L}$$

where $\hat{D}$ is the estimated density of dolphin schools in the survey area based on the number of schools observed, N, over transect length L. The function $f(x)$ is a probability density function fit to the observed perpendicular sighting distances and estimating its value at zero distance, $\hat{f}(0)$, is the critical concern in the application of line-transect methods (Burnham et al. 1980).

The frequency distribution of observed perpendicular sighting distances reflects both the detection abilities of the observer and the reactions of the observed (Burnham et al. 1980). Dolphin schools are more difficult to see with distance from the track line and avoidance, prior to detection, may cause fewer schools to be seen close to the track line and more schools to be seen further from the track line. The school that did move away from the transect line before shipboard detection (#8) would have been sighted at 0.1 nmi off the transect line if it had not altered the direction of its movement. Instead it was detected at 1.0 nmi off the transect line. If the sample size was larger, such information could be used to dissect the frequency distribution of perpendicular sighting distances into that component which is the result of decreasing visibility with distance from the transect line and that component which is the result of dolphin schools adjusting their natural spatial disposition

TABLE 2.—Comparison of shipboard and aerial estimates of dolphin school size and species composition.

	Vessel estimate				Helicopter estimate			
School number	Number of observers	Estimated number of individuals (standard error)	Species proportions (range)		Number of observers	Estimated number of individuals	Species proportions	
20	5	248 (24)	*S. attenuata*	0.14 (0.05-0.20)	1	260	*S. attenuata*	0.15
			S. longirostris	0.86 (0.80-0.95)			*S. longirostris*	0.85
22	4	241 (40)	*S. attenuata*	0.96 (0.90-1.00)	1	180	*S. attenuata*	0.50
			S. longirostris	0.04 (0.00-0.10)			*S. longirostris*	0.50
23	4	139 (20)	*S. attenuata*	0.62 (0.50-0.73)	1	155	*S. attenuata*	0.50
			S. longirostris	0.35 (0.22-0.50)			*S. longirostris*	0.50
			Unidentified	0.03 (0.00-0.12)				
24	6	36 (6)	*S. coeruleoalba*	1.00 (1.00-1.00)	1	29	*S. coeruleoalba*	1.00
25	5	393 (61)	*S. attenuata*	0.55 (0.40-0.70)	1	410	*S. attenuata*	0.40
			S. longirostris	0.39 (0.30-0.60)			*S. longirostris*	0.60
			Unidentified	0.06 (0.00-0.30)				
26[1]	5	55 (9)	*S. attenuata*	1.00 (1.00-1.00)	1	85	*S. attenuata*	1.00

[1]Not detected by shipboard observers while in survey mode; ship was directed to school by aerial observer.

in response to the ship. There are, however, other factors (such as glare and sea state) which are seldom constant long enough to allow for accumulation of a reasonably precise frequency distribution, such that the effects due to school movement would not be overwhelmed by the effects due to sighting conditions.

The results of this experiment suggest that 1) dolphin schools occasionally react to the approach of a survey vessel prior to their detection by shipboard observers and 2) the expected rarity of the event implies that a considerable amount of additional data would be required to quantify its effect.

Any directed movement prior to detection biases the frequency distribution of perpendicular distances and may bias the function, $f(x)$, fit to these data. In the absence of information regarding movement, Burnham et al. (1980) suggested choosing a function which is relatively insensitive to data contaminated by movement, i.e., a function that monotonically decreases with distance from the transect line. Their simulations suggest that in situations where "undetected movement is relatively minor, then use of an estimator based on a monotonically decreasing function will minimize bias in $\hat{D}$." (Burnham et al. 1980:130). The small sample size of the present experiment was sufficient to qualify undetected movement as relatively minor but not sufficient to quantify its effect on the distribution of perpendicular distances.

Although the work reported here was conducted in the same geographic area (Clipperton Island, lat. 10° N, long. 110° W) as the Au and Perryman (1982) observations, the two experiments are not strictly comparable. Au and Perryman used the ship and helicopter to search for schools and collected data on their reaction to the ship without regard to the effect on survey operations; in four of the eight schools they studied, the ship was turned toward the school during tracking. They were interested in describing the behavior of dolphin schools and combining the description with a search model to quantify survey bias. The present experiment did not assume that the two processes (reaction and detection) were independent and was less ambitious because there was no intention to generalize dolphin behavior. Indeed, the results presented here may only be relevant to this area and for these sighting conditions. Both the reaction distance and the sighting distance may be affected by environmental conditions and may vary between geographic areas with the degree of animal naivete.

The comparisons of aerial and shipboard results suggest that school-size estimates may be more reliable than those of species composition. Although neither observation platform can be considered to yield estimates without error, they do provide unique vantage points with very different views of the dolphin school. All shipboard observers, after exposure to observation conditions in the helicopter, agreed that they could more confidently estimate school size from the air than from a vessel. The helicopter provides an opportunity to observe the entire school over an extended period of time, making it easier to estimate that portion of the school which is submerged and not completely visible. Species proportions are more difficult to estimate and it is not clear which platform is better; indeed, in the case of school 22, all four shipboard observers reported similar proportions which were quite different than that estimated from the air. One explanation may be that it is more difficult to identify animals in plan view than in profile view; alternately, the fluid character of school structure may combine with the limited view of the school from a ship to preclude accurate estimates of species proportions; a third possibility is that both are inaccurate because of species-specific behaviors which make the animals less visible from above and/or the side.

Estimates of the density of dolphin schools are multiplied by the area of the survey, the average school size and the species proportions to estimate species abundances (Holt and Powers 1982). Because they affect the abundance estimates directly, biases in the latter two parameters may be more serious than the effect of school movement prior to detection. As an example, consider the six schools compared during this experiment: the average number of *S. attenuata* per school, estimated by shipboard observers, was 27% greater than that estimated from the helicopter data, the shipboard estimate of *S. longirostris* was 34% less than the helicopter estimates, and the estimate of *S. coeruleoalba* was the same for both platforms (Table 3). Although these differences should only be considered as variability between two estimates, they illustrate the direct dependence of abundance estimates on accurate estimates of species proportions. Avoidance affects density estimates less dramatically; its affect on $\hat{f}(0)$ may be somewhat offset by using a function that is relatively insensitive to predetection movement.

The application of line-transect methods requires that along the transect line all schools are seen with certainty. Any departures from the assumption of perfect detection, either because of

TABLE 3.—Average dolphin school composition.

	Vessel	Helicopter
Average school size (number of individuals)	185.3	186.5
Average species proportions		
S. attenuata	0.545	0.425
S. longirostris	0.273	0.408
S. coeruleoalba	0.167	0.167
Unidentified dolphin	0.015	
Average school composition[1]		
S. attenuata	102.5	79.3
S. longirostris	51.3	76.1
S. coeruleoalba	31.5	31.1

[1]Unidentified dolphins distributed proportionately among identified dolphins following Holt and Powers (1982).

movement or visibility effects, will introduce a negative bias in the density estimate that is proportional to the decrease in apparent density along the transect line (Smith 1979). The sample size was insufficient to test this assumption rigorously; only one school was observed on the transect line (school 14) and it was detected well beyond any of the reaction distances observed.

It is recommended that future fieldwork include additional comparisons of estimates of school size and species proportions. In addition, the assumption of certain detection along the transect line should be tested. Biases in school composition and detection on the transect line affect the abundance estimates directly and present a greater potential for inaccuracy than the degree of directed movement prior to detection observed during this experiment.

ACKNOWLEDGMENTS

This work was accomplished with the help and collaboration of several people: D. Au, D. Chapman, P. Hammond, J. Laake, and W. Perryman generously gave their time and advice during the design of the experiment; and the conscientious and competent field observers included G. Friedrichsen in the helicopter, A. Jackson, W. Irwin, and M. Noel on the NOAA ship *Surveyor*, and J. Cotton, J. Doxey, M. Henry, M. Graybill, R. Pitman, and G. Yee lead by W. Parks on the NOAA Ship *David Starr Jordan*. R. Holt, T. Jackson, W. Perrin, and P. Vergne reviewed the manuscript. The final draft benefited from the comments of two anonymous reviewers.

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FIN EROSION AMONG FISHES COLLECTED NEAR A SOUTHERN CALIFORNIA MUNICIPAL WASTEWATER OUTFALL (1971-82)[1]

JEFFREY N. CROSS[2]

ABSTRACT

In the Southern California Bight, fin erosion is most frequently encountered among fishes collected near municipal wastewater outfalls. This paper presents an analysis of the trends in the incidence of fin erosion among fishes collected by otter trawls near Los Angeles from 1971 through 1982.

About 24% of the 122 species of fish and 9% of the more than 170,000 individuals collected had the disease. Flatfish (Pleuronectidae, Bothidae, and Cynoglossidae) and rockfish (Scorpaenidae) accounted for 66% of the affected species and 99% of the affected individuals. Dover sole (Pleuronectidae: *Microstomus pacificus*) accounted for 89% of the affected individuals.

The incidence of fin erosion was highest close to the outfalls and declined with increasing distance. The number of species with the disease declined from 1971 to 1982. The incidence of the disease also declined in two of the three most affected species (Dover sole and rex sole, *Glyptocephalus zachirus*). The contemporaneous decline in the number of species and the proportion of individuals with the disease and the decline in surface sediment contaminant levels suggest that the magnitude of contamination and the incidence of fin erosion are directly related.

The effect of fin erosion on the Dover sole population was examined. Dover sole recruit to the study area when they are 40-50 mm SL; the incidence of fin erosion was negligible in new recruits but increased rapidly with increasing fish size. No significant differences were detected in the length-weight relationships or size-at-age data between Dover sole with and without the disease. Survival rates of Dover sole with and without fin erosion were similar until age 3; thereafter, the survival rate of diseased fish was significantly lower.

Fin erosion in the Southern California Bight is most prevalent in fish collected near major municipal wastewater outfalls. Of the major outfalls, the disease is most frequently encountered around the Joint Water Pollution Control Project (JWPCP) outfalls on the Palos Verdes shelf (Mearns and Sherwood 1974, 1977; Sherwood and Mearns 1977). About 20% of the 151 species of fish collected in the Southern California Bight between 1969 and 1976 were affected by the disease. Flatfish (Pleuronectidae, Bothidae, and Cynoglossidae) and rockfish (Scorpaenidae) accounted for 60% of the affected species and 97% of the affected individuals (Mearns and Sherwood 1977; Sherwood 1978).

Municipal wastewater discharge on the Palos Verdes shelf began in the late 1930's. The mass emission of suspended solids increased steadily from about 17,000 metric tons (t) in the early 1940's to a peak of 167,000 t in 1971 (Wilson et al. 1980). Awareness of the problem of discharging excessive amounts of solids and associated contaminants by JWPCP in the early 1970's resulted in the installation of new equipment and more effective treatment procedures to reduce solid emissions. By 1981, discharge of suspended solids had declined to 84,000 t. The mass emission of contaminants also declined from 1971 to 1981 (Schafer 1982). Otter trawling, as part of a regular monitoring program of the animals on the Palos Verdes shelf, began in 1971.

The purpose of this paper is to determine trends in the incidence of fin erosion among fish collected by otter trawls near the JWPCP outfalls from 1971 through 1982. The prevalence of the disease over the size range of individuals collected and the effect of the disease on growth and survival are examined for the most affected species.

METHODS

The data analyzed in this study were collected by the Los Angeles County Sanitation District (LACSD) during regular monitoring cruises on the Palos Verdes shelf; station and transect identifications used herein are LACSD designations. Daytime trawls were made at three depths (23, 61, and

[1]Contribution No. 196, Southern California Coastal Water Research Project.

[2]Southern California Coastal Water Research Project, 646 W. Pacific Coast Highway, Long Beach, CA 90806.

Manuscript accepted April 1984.
FISHERY BULLETIN: VOL. 83, NO. 2, 1985.

137 m) at each of seven transects (Fig. 1) with an otter trawl towed along a depth isobath at 1.1 m/s for 10 min. A 7.3 m (headrope length) trawl was used from 1971 to 1974, when it was replaced by a 7.6 m net; a 1.25 cm mesh cod end liner was used in both nets. From 1971 through 1978, two samples—one between April and June and one between October and December—were collected annually at each depth; occasionally, additional trawls were made and these were included in the analyses. Quarterly trawling began in 1979 and has continued to the present. Sampling was discontinued at transects T2, T3, and T6 in 1977.

Trawl catches were sorted by species and processed on board ship. The standard length of each individual was determined on a measuring board (BSL = board standard length). External abnormalities (e.g., fin erosion, parasites, tumors) were recorded along with length.

Trends in the incidence of fin erosion per 10-min trawl were determined from linear regressions of the proportion (p) of fish with the disease (transformed to arcsin $\sqrt{p}$) versus time [numbered in consecutive months from 1971 through 1982 (i.e., 1, 2, 3, ..., 143, 144)]. Collections where only one individual of the species of interest was caught were dropped from the analysis because the resulting transformed datum (either 0 or 90) often had a large effect on the residual sum of squares. Trends in the total catch per 10-min trawl were determined from linear regressions of numbers [transformed to $\log_{10}(x + 1)$] versus time. The null hypothesis that the regression function (slope) was equal to zero was tested with a t-test. The null hypothesis of equality of the regression functions was tested by analysis of covariance (ANCOVA). If the null hypothesis was not accepted, significant differences were detected with a Newman-Keuls multiple range test (Zar 1974). Calico rockfish, *Sebastes dalli*, rex sole, *Glyptocephalus zachirus*, and Dover sole, *Microstomus pacificus*, accounted for 96.6% of the fish with fin erosion (Table 1) so the trend analysis was performed on each species individually. Less than 1% of the fin eroded fish came from the 23 m stations; these stations were then dropped from the analyses.

The quarterly trawl data (1979-82) from transects T4 and T5 were examined for seasonal trends in the total catch of Dover sole, the number with fin erosion, and the proportion with fin erosion with the following model:

$$Y_t = f(T_t, S_t) + \epsilon_t$$

where Y_t = observed abundance (or proportion) in period t, T_t = trend factor of time series in period t, S_t = seasonal factor of time series in period t, f = function relating observed abundance (or proportion) to the trend and seasonal components, and ϵ_t = irregular factor of time series in period t (Bowerman and O'Connell 1979). Multiplicative and additive models were fitted to the quarterly trawl data after transformation [$\log_{10}(x + 1)$ and arcsin $\sqrt{p}$]. Multiplicative models gave the best fit (lowest residual sum of squares) so only those results are presented. After determining the quarterly trends, the original transformed data were "deseasonalized" by dividing each value by the corresponding seasonal factor. Trends in the de-

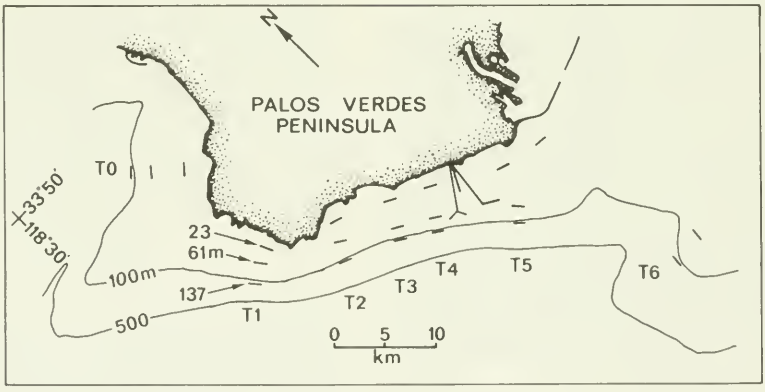


FIGURE 1.—Location of sampling transects on the Palos Verdes shelf. Three depths (23, 61, and 137 m) were sampled at each transect. Joint Water Pollution Control Project outfalls are located between transects T4 and T5. Net current flow is northwest.

TABLE 1.—Taxonomic list of fish affected with fin erosion collected in 622 otter trawls on the Palos Verdes shelf from 1971 through 1982.

Common name	Scientific name	Number collected	Frequency of occurrence (%) in trawl collections	Percent with fin erosion	Percent of all fish with fin erosion
spotted cusk-eel	*Chilara taylori*	191	16.7	0.5	<0.1
blackbelly eelpout	*Lycodopsis pacifica*	2,629	20.6	0.1	0.1
shortspine thornyhead	*Sebastolobus alascanus*	312	4.3	1.9	<0.1
calico rockfish	*Sebastes dallii*	9,153	23.6	9.9	5.8
shortbelly rockfish	*Sebastes jordani*	3,247	25.1	0.2	0.1
stripetail rockfish	*Sebastes saxicola*	18,938	54.5	0.1	0.1
vermillion rockfish	*Sebastes miniatus*	382	17.1	0.5	<0.1
pink rockfish	*Sebastes eos*	37	1.1	5.4	0.1
greenstriped rockfish	*Sebastes elongatus*	263	13.8	2.3	0.1
splitnose rockfish	*Sebastes diploproa*	6,973	24.0	<0.1	<0.1
sablefish	*Anoplopoma fimbria*	711	15.6	0.3	0.1
shortspine combfish	*Zaniolepis frenata*	794	20.6	0.1	<0.1
longspine combfish	*Zaniolepis latipinnis*	891	20.7	0.4	0.1
barred sand bass	*Paralabrax nebulifer*	40	4.0	2.5	<0.1
white croaker	*Genyonemus lineatus*	9,062	20.9	1.6	0.9
white seaperch	*Phanerodon furcatus*	848	12.1	0.2	<0.1
shiner perch	*Cymatogaster aggregata*	9,478	27.1	0.1	<0.1
Pacific pompano	*Peprilus simillimus*	30	2.0	20.0	<0.1
California tonguefish	*Symphurus atricauda*	1,091	25.4	1.7	0.1
Pacific sanddab	*Citharichthys sordidus*	11,698	61.3	0.5	0.4
speckled sanddab	*Citharichthys stigmaeus*	15,491	39.6	<0.1	<0.1
bigmouth sole	*Hippoglossina stomata*	148	14.6	2.1	<0.1
C-O sole	*Pleuronichthys coenosus*	187	10.8	1.1	<0.1
curlfin sole	*Pleuronichthys decurrens*	3,774	40.4	2.4	0.6
hornyhead turbot	*Pleuronichthys verticalis*	458	25.0	1.1	<0.1
English sole	*Parophrys vetulus*	1,256	44.7	0.9	<0.1
rex sole	*Glyptocephalus zachirus*	4,452	28.0	6.7	1.9
slender sole	*Lyopsetta exilis*	4,674	26.0	3.3	1.0
Dover sole	*Microstomus pacificus*	41,627	62.2	33.5	88.9

seasonalized data were determined by linear regression.

The effects of fin erosion on the population of Dover sole on the Palos Verdes shelf were examined using the original data of Mearns and Harris (1975)[3] that consisted of length, weight, sex, and age (from otoliths) of 328 Dover sole collected in 1972 and 1973.

Size-frequency distributions between Dover sole of the same age with and without fin erosion were compared with a Kolmogorov-Smirnov two sample test (Siegel 1957). A one-tailed test was used because the disease might be expected to reduce the growth rate of affected individuals.

Weight-length relationships among male and female Dover sole with and without fin erosion were compared with the geometric mean regression

$$\log w = \log a + b\ (\log l)$$

where w = weight, l = length, and a and b are fitted constants (Ricker 1973). The regression coefficients were compared statistically using the method of Clarke (1980).

The survival rate of Dover sole with and without fin erosion was compared. Using an age-length key developed from the data, ages were assigned to all Dover sole captured in LACSD monitoring trawls on the Palos Verdes shelf from 1972 through 1975. Survival rate (S) was calculated from age t (in years) to age $t + 1$ from

$$S = \frac{N_{t+1}}{N_t}$$

where N = the number caught (Ricker 1975). Survival rates of fish with and without the disease were compared with a t-test after the data were transformed to the reciprocal ($1/x$) to stabilize the variance. A one-tailed test was used because the disease might be expected to reduce the survival rate of affected individuals.

RESULTS

From 1971 through 1982, LACSD made 622 monitoring trawls on the Palos Verdes shelf. Fin erosion was reported for 15,680 individuals (9.2% of all individuals collected) representing 29 species (23.8% of all species collected) (Table 1).

[3]Mearns, A. J., and L. Harris. 1975. Age, length, and weight relationships in southern California populations of Dover sole. Tech. Memo. 219, 17 p. Southern California Coastal Water Research Project, Long Beach.

Flatfish (Pleuronectidae, Bothidae, and Cynoglossidae) and rockfish (Scorpaenidae) accounted for 65.5% of the affected species and 99.2% of the affected individuals; Dover sole (Pleuronectidae) accounted for 88.9% of the affected individuals.

The number of species affected by fin erosion declined from a high of 18 in 1971 to a low of 3 in 1981 (Fig. 2); the decrease was highly significant ($r = -0.766$, $n = 12$, $0.002 < P < 0.005$). There was no significant change in the number of species collected over the same period (Fig. 2) ($r = -0.291$, $n = 12$, $0.20 < P < 0.50$).

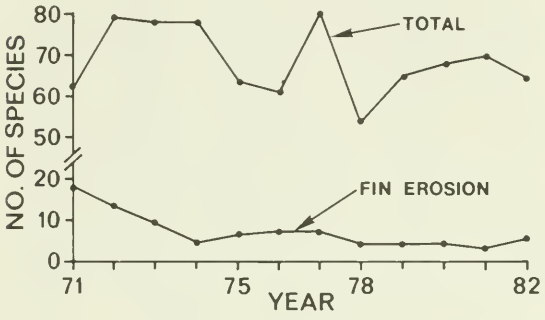


FIGURE 2.—Annual total number of fish species collected and number with fin erosion collected by otter trawl on the Palos Verdes shelf from 1971 to 1982.

CALICO ROCKFISH

Calico rockfish, *Sebastes dallii*, were rarely collected before 1975. Beginning in 1975, they were collected at all stations; the majority (72.4%) were collected at 61 m. Ten percent of the individuals collected had fin erosion; as a species, they accounted for 6% of all fish with the disease (Table 1). The incidence of fin erosion among calico rockfish increased at all 61 m stations from 1975 to 1982, but the increase was not significant at T0 (Table 2). ANCOVA detected a significant difference among the regression coefficients of the 61 m stations ($F = 5.02$, $0.003 < P < 0.005$) (Table 3).

The total number of calico rockfish collected in a 10-min trawl at 61 m decreased significantly at T4, but did not change at T0, T1, and T5 (Table 2). The regression coefficients for these collections were not significantly different ($F = 1.02$, $P > 0.25$).

REX SOLE

Seven percent of the rex sole, *Glyptocephalus zachirus*, had fin erosion; as a species, they accounted for 2% of all fish with the disease (Table 1). More than 99% of the rex sole collected were caught at 137 m. Less than 1% of the fish collected at station T0-137 m had fin erosion. The incidence of fin erosion among rex sole at the remaining 137 m stations declined significantly (Table 4). ANCOVA did not detect a significant difference among the regression coefficients for these collections ($F = 1.05$, $P > 0.25$).

The number of rex sole caught in a 10-min trawl at the 137 m stations did not change over the study period (Table 4), and the regression coefficients for these collections were not significantly different ($F = 1.43$, $0.10 < P < 0.25$).

DOVER SOLE

Dover sole, *Microstomus pacificus*, was by far the most affected species. Thirty-four percent of Dover sole collected had fin erosion; as a species, they accounted for 89% of all fish with the disease (Table 1). The incidence of fin erosion among Dover sole declined significantly at all stations except T0-137 m (Table 5). ANCOVA detected a significant difference among the regression coefficients

TABLE 2.—Linear regressions of A) the proportion (p) of calico rockfish, *Sebastes dallii*, in one 10-min trawl with fin erosion (transformed to arcsin $\sqrt{p}$) and B) the total number of calico rockfish caught in one 10-min trawl [transformed to $\log_{10}(x + 1)$] against time (numbered in consecutive months from 1971 through 1982). n = sample size; L1 = lower limit of 95% confidence interval of the regression coefficient (b); L2 = upper limit; P = probability that b came from a sampling population with $\beta = 0$.

	Station	$\hat{Y} = a + bX$	n	L1	L2	P
A)	T0-61 m	$Y = -0.384 + 0.010X$	23	−0.020	0.040	$0.20 > P > 0.50$
	T1-61 m	$Y = -7.325 + 0.125X$	26	0.021	0.229	$P = 0.02$
	T4-61 m	$Y = -41.950 + 0.678X$	19	0.178	1.178	$0.01 < P < 0.02$
	T5-61 m	$Y = -20.150 + 0.410X$	21	0.070	0.751	$0.02 < P < 0.05$
B)	T0-61 m	$Y = 1.808 - 0.0027X$	25	−0.0150	0.0096	$P > 0.50$
	T1-61 m	$Y = 1.681 - 0.0015X$	27	−0.0115	0.0085	$P > 0.50$
	T4-61 m	$Y = 1.888 - 0.0098X$	26	−0.0194	−0.0002	$0.02 < P < 0.05$
	T5-61 m	$Y = 0.756 + 0.0021X$	26	−0.0076	0.0118	$P > 0.50$

of these collections ($F = 17.84, P < 0.0001$) (Table 6).

The total number of Dover sole collected in a 10-min trawl declined significantly at three of the eight stations (Table 5). ANCOVA detected a significant difference among the regression coefficients of these collections ($F = 3.43$, $0.001 < P < 0.003$) (Table 6).

TABLE 3.—Results of Newman-Keuls multiple range test for equality of regression coefficients (b) for the incidence of fin erosion among calico rockfish. s = station; underscored stations are not significantly different.

b:	0.678	0.410	0.125	0.010
s:	T4-61 m	T5-61 m	T1-61 m	T0-61 m

Size-Frequency Distributions

The size distributions of Dover sole with and without fin erosion were examined (Fig. 3). Most Dover sole recruit to the study area when they are 40-50 mm BSL (broad standard length). Fin ero-

TABLE 4.—Linear regressions of A) the proportion (p) of rex sole, *Glyptocephalus zachirus*, in one 10-min trawl with fin erosion (transformed to arcsin $\sqrt{p}$) and B) the total number of rex sole caught in one 10-min trawl [transformed to $\log_{10}(x + 1)$] against time (numbered in consecutive months from 1971 through 1982). See Table 2 for explanation of column headers.

	Station	$\hat{Y} = a + bX$	n	L1	L2	P
A)	T0-137 m	[only 7 of 1,520 fish (0.5%) had fin erosion]				
	T1-137 m	$Y = 10.217 - 0.085X$	33	−0.132	−0.038	$0.002 < P < 0.005$
	T4-137 m	$Y = 18.259 - 0.151X$	35	−0.239	−0.064	$0.001 < P < 0.002$
	T5-137 m	$Y = 10.733 - 0.087X$	29	−0.151	−0.023	$P = 0.01$
B)	T0-137 m	$Y = 1.828 - 0.0038X$	33	−0.0081	0.0005	$0.05 < P < 0.10$
	T1-137 m	$Y = 1.326 - 0.0012X$	33	−0.0053	0.0029	$P > 0.50$
	T4-137 m	$Y = 0.976 + 0.0023X$	36	−0.0020	0.0066	$0.20 < P < 0.50$
	T5-137 m	$Y = 1.182 - 0.0013X$	32	−0.0064	0.0038	$P > 0.50$

TABLE 5.—Linear regressions of A) the proportion (p) the Dover sole, *Microstomus pacificus*, in one 10-min trawl with fin erosion (transformed to arcsin $\sqrt{p}$) and B) the total number of Dover sole caught in one 10-min trawl [transformed to $\log_{10}(x + 1)$] against time (numbered in consecutive months from 1971 through 1982). See Table 2 for explanation of column headers.

	Station	$\hat{Y} = a + bX$	n	L1	L2	P
A)	T0-61 m	$Y = 0.861 - 0.0076X$	29	−0.0148	−0.0004	$0.02 < P < 0.05$
	T0-137 m	$Y = 0.907 - 0.0047X$	33	−0.0120	0.0026	$P = 0.20$
	T1-61 m	$Y = 29.526 - 0.240X$	24	−0.308	−0.172	$P << 0.001$
	T1-137 m	$Y = 28.048 - 0.201X$	33	−0.274	−0.128	$P << 0.001$
	T4-61 m	$Y = 54.520 - 0.332X$	29	−0.511	−0.154	$P < 0.001$
	T4-137 m	$Y = 48.157 - 0.224X$	36	−0.336	−0.112	$P < 0.001$
	T5-61 m	$Y = 54.732 - 0.374X$	31	−0.482	−0.266	$P << 0.001$
	T5-137 m	$Y = 38.618 - 0.214X$	30	−0.300	−0.128	$P << 0.001$
B)	T0-61 m	$Y = 1.601 - 0.0075X$	37	−0.0128	−0.0022	$0.005 < P < 0.01$
	T0-137 m	$Y = 1.981 - 0.0017X$	34	−0.0066	0.0032	$P > 0.50$
	T1-61 m	$Y = 1.603 - 0.0077X$	34	−0.0136	−0.0018	$0.01 < P < 0.02$
	T1-137 m	$Y = 2.432 - 0.0072X$	34	−0.0115	−0.0029	$0.001 < P < 0.002$
	T4-61 m	$Y = 0.688 + 0.0043X$	40	−0.0010	0.0096	$0.10 < P < 0.20$
	T4-137 m	$Y = 2.118 - 0.0007X$	36	−0.0044	0.0030	$P > 0.50$
	T5-61 m	$Y = 1.354 - 0.0018X$	39	−0.0067	0.0031	$0.20 < P < 0.50$
	T5-137 m	$Y = 2.592 - 0.0037X$	31	−0.0082	0.0008	$P = 0.10$

TABLE 6.—Results of Newman-Keuls multiple range test for equality of regression coefficients (b) for A) the proportion of Dover sole, *Microstomus pacificus*, with fin erosion and B) the total catch of Dover sole. s = station; underscored stations are not significantly different.

A) b:	−0.374	−0.332	−0.240	−0.224	−0.214	−0.201	−0.008	−0.005
s:	T5-61 m	T4-61 m	T1-61 m	T4-137 m	T5-137 m	T1-137 m	T0-61 m	T0-137 m
B) b:	−0.0043	−0.0007	−0.0017	−0.0018	−0.0037	−0.0072	−0.0075	−0.0077
s:	T4-61 m	T4-137 m	T0-137 m	T5-61 m	T5-137 m	T1-137 m	T0-61 m	T1-61 m

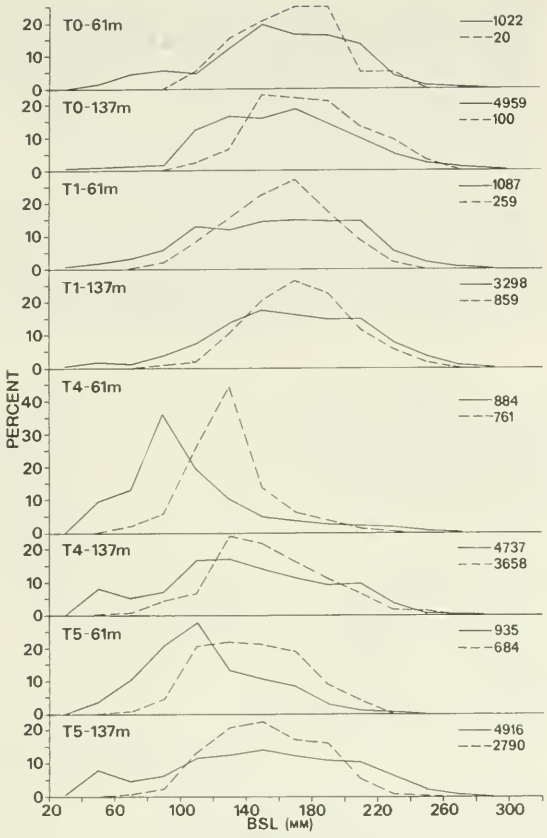


FIGURE 3.—Size distributions of Dover sole, *Microstomus pacificus*, with fin erosion (dashed line) and without fin erosion (solid line) by 20 mm size class (i.e., 20-39 mm, 40-59 mm, ..., 300-319 mm) for all collections (1971-82) combined. The number of individuals is presented to the right. BSL = board standard length.

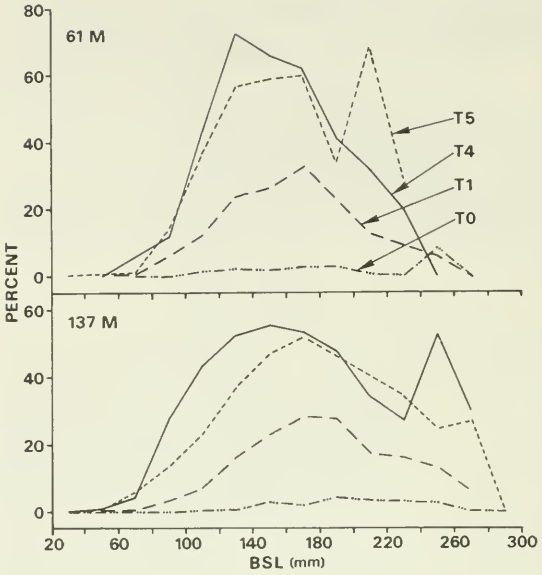


FIGURE 4.—Percent of Dover sole, *Microstomus pacificus*, with fin erosion in each 20 mm size class (i.e., 20-39 mm, 40-59 mm, ..., 280-299 mm) at 61 m and 137 m on the sampling transects. Data for each station are 12-yr totals. BSL = board standard length.

sion was observed in 0.3% of the fish between 40 and 59 mm BSL, 3.8% of the fish between 60 and 79 mm BSL, and 17.7% of the fish between 80 and 99 mm BSL. The incidence of fin erosion peaked in fish 120-139 mm BSL at stations close to the outfalls, and in fish 140-179 mm BSL at more distant stations. The proportion of fish with fin erosion in a particular size class was greatest at stations close to the outfalls and declined progressively with increasing distance (Fig. 4).

Seasonal Trends

Time series analyses of the quarterly trawl data (1979-82) for Dover sole at T4 and T5 showed consistent seasonal peaks in the total catch and in the number of individuals with fin erosion, but not in the proportion of individuals with the disease (Fig. 5). The seasonal indices of total catch and number with fin erosion were highest in the second (April-June) and third (July-September) quarters at 61 m and in the third and fourth quarters at 137 m. The magnitude of the seasonal swing was greater at 61 m.

Examination of the deseasonalized data revealed that there was no change in the total catch of Dover sole, the number of individuals with fin erosion, or the proportion of individuals with fin erosion at 61 m between 1979 and 1982 (Table 7). At 137 m, there was a significant decline in the number of Dover sole with fin erosion at T4 and T5, and a significant decline in the total catch and proportion of individuals with fin erosion at T4 (Table 7).

Size at Age

The Mearns and Harris (footnote 3) data were examined for differences in the size-frequency distributions between Dover sole with and without fin erosion at a particular age. There were no significant differences for fish age 2 ($\chi^2 = 0$, df = 2, $P > 0.90$), age 3 ($\chi^2 = 1.27$, df = 2, $0.50 < P < 0.70$), age 4 ($\chi^2 = 1.71$, df = 2, $0.30 < P < 0.50$), or age 5 ($\chi^2 = 2.12$, df = 2, $0.30 < P < 0.50$).

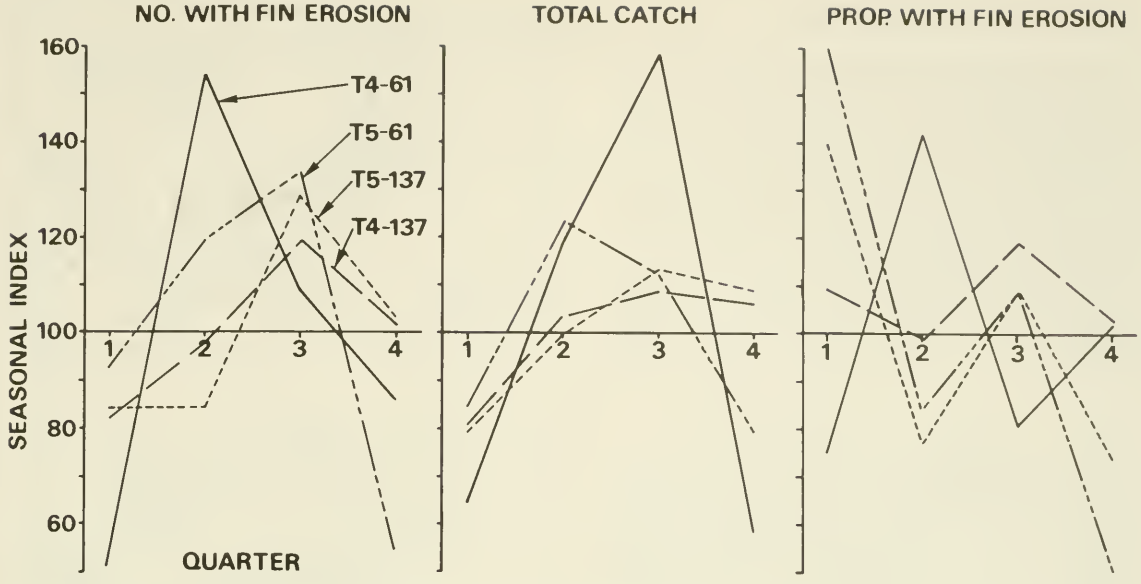


FIGURE 5.—Quarterly seasonal trends in the total catch of Dover sole, *Microstomus pacificus*, the number of individuals with fin erosion, and the proportion of individuals with fin erosion collected at 61 m and 137 m at T4 and T5 from 1979 through 1982. Quarter 1 = Jan.-Mar., 2 = Apr.-June, 3 = July-Sept., 4 = Oct.-Dec.

TABLE 7.—Linear regressions of the deseasonalized A) total catch of Dover sole, *Microstomus pacificus*, in one 10-min trawl [transformed to $\log_{10}(x+1)$], B) number of Dover sole with fin erosion [transformed to $\log_{10}(x+1)$], and C) proportion (p) of Dover sole with fin erosion (transformed to arcsin $\sqrt{p}$) regressed against time (numbered in consecutive quarters from 1979 through 1982). See Table 2 for explanation of column headers.

	Station	$\hat{Y}_t = a + bt$	n	L1	L2	P
A)	T4-61 m	$Y_t = 1.176 + 0.014t$	16	−0.057	0.085	$P > 0.50$
	T4-137 m	$Y_t = 2.467 - 0.036t$	16	−0.069	−0.003	$0.02 < P < 0.05$
	T5-61 m	$Y_t = 1.303 - 0.007t$	16	−0.082	0.068	$P > 0.50$
	T5-137 m	$Y_t = 2.509 - 0.041t$	16	−0.115	0.033	$0.05 < P < 0.10$
B)	T4-61 m	$Y_t = 0.370 + 0.043t$	16	−0.028	0.114	$0.20 < P < 0.50$
	T4-137 m	$Y_t = 2.303 - 0.075t$	16	−0.121	−0.029	$0.002 < P < 0.005$
	T5-61 m	$Y_t = 0.708 + 0.002t$	16	−0.056	0.060	$P > 0.50$
	T5-137 m	$Y_t = 2.082 - 0.067t$	16	−0.121	−0.013	$0.01 < P < 0.02$
C)	T4-61 m	$Y_t = 22.09 + 0.350t$	16	−1.616	2.316	$P > 0.50$
	T4-137 m	$Y_t = 48.45 - 1.470t$	16	−2.819	−0.121	$0.02 < P < 0.05$
	T5-61 m	$Y_t = 29.32 - 0.267t$	16	−2.055	1.521	$P > 0.50$
	T5-137 m	$Y_t = 40.87 - 0.982t$	16	−2.635	0.671	$0.20 < P < 0.50$

Weight-Length Relationships

The Mearns and Harris data were examined for differences in the weight-length relationships among males and females with and without fin erosion. There were no significant differences in the regression coefficients between males with and without the disease ($T_{12} = 1.587$, df = 38, $0.10 < P < 0.20$) and between females with and without the disease ($T_{12} = 0.508$, df = 56, $P > 0.50$) (Table 8). There was a significant difference between males and females without the disease ($T_{12} = 3.189$, df = 64, $0.002 < P < 0.005$), but not between males and females with the disease ($T_{12} = 0.713$, df = 37, $0.20 < P < 0.50$).

TABLE 8.—Results of the geometric mean regression of $\log w = \log a + b(\log l)$, where w = weight and l = length, for male and female Dover sole with and without fin erosion. L1 = lower limit of 95% confidence interval of the regression coefficient (b); L2 = upper limit.

Fin erosion	$\log w = \log a + b(\log l)$	L1	L2
Males without	$\log w = -4.514 + 2.864(\log l)$	2.663	3.065
Males with	$\log w = -4.994 + 3.114(\log l)$	2.852	3.376
Females without	$\log w = -5.564 + 3.310(\log l)$	3.116	3.504
Females with	$\log w = -5.379 + 3.234(\log l)$	3.002	3.466

Survival Rates

The survival rates of Dover sole with and without fin erosion from Palos Verdes were not significantly different from age 1 to age 2 ($t = 1.267$, df $= 4$, $0.10 < P < 0.25$) and from age 2 to age 3 ($t = 0.741$, df $= 4$, $P = 0.25$) (Fig. 6). The survival rates were significantly lower for individuals with fin erosion from age 3 to age 4 ($t = 2.826$, df $= 4$, $0.01 < P < 0.025$) and from age 4 to age 5 ($t = 2.890$, df $= 4$, $0.01 < P < 0.025$). No individuals with fin erosion older than age 5 were collected (Fig. 6).

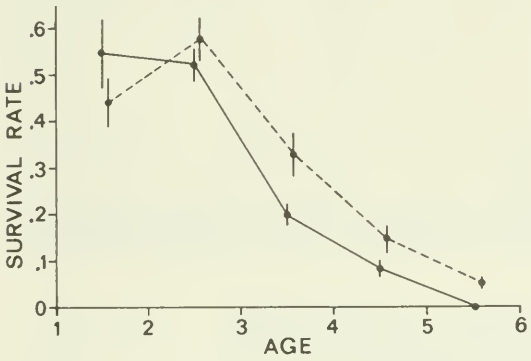
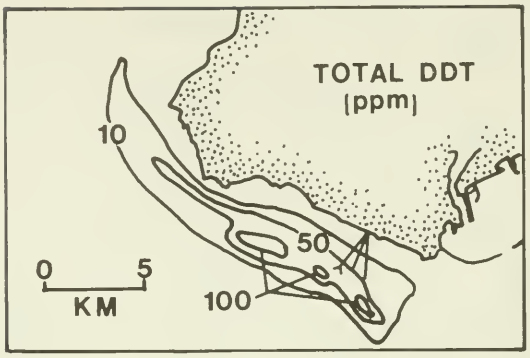


FIGURE 6.—Survival rate of Dover sole, *Microstomus pacificus*, with fin erosion (solid line) and without fin erosion (dashed line) from year t to year $t + 1$. Data presented as mean and 1 SE (vertical line).



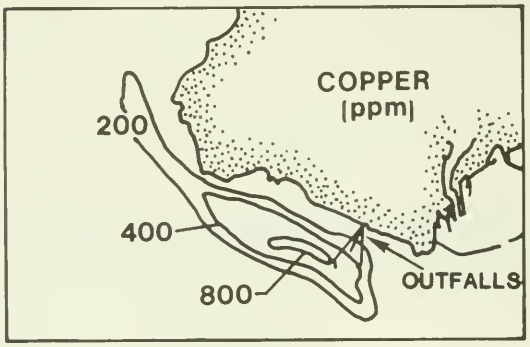


FIGURE 7.—Contour maps of total DDT (ppm dry weight) and copper (ppm dry weight) concentrations in surface sediments on the Palos Verdes shelf in 1975. Maps redrawn from Hershelman et al. (1977).

DISCUSSION

Current and Sediment Characteristics on the Palos Verdes Shelf

Near the outfalls, the net current movement 20 m from the bottom in 61 m of water is 5.5 cm/s upcoast (northwest). Both net flow and major current fluctuations are oriented in the upcoast direction (Hendricks 1980). Sewage particles suspended in freshwater are discharged from the outfalls, rise in the water column, and are carried generally upcoast as they settle back to the bottom. Trace metal and chlorinated hydrocarbon contaminants measured in surface sediments reveal the characteristic "footprint" of the settled particles (Fig. 7) (Young and Heesen 1978; Young et al. 1978). The concentrations of DDT (Table 9), trace metals (Table 10), and organic material (Table 11) in surface sediments are highest around the outfalls and decline upcoast, and generally have declined during the study period.

TABLE 9.—Total DDT concentration (ppm dry weight) of surface sediments at the sampling transects from 1972 to 1981. Note that the deeper samples were taken at 152 m while the trawls were made at 137 m. Depth of sediments analyzed at bottom of the table. (SCCWRP and LACSD, unpubl. data.)

	Year							
Station	1972	1973	1975	1977	1979	1980	1981	1982
T0-30 m		0.9				0.3		
T0-61 m		2.6	3.5			1.3	1.9	
T0-152 m		2.6	3.7			1.6		
T1-61 m		160	62		11	13	4	
T1-152 m		55	17					
T4-30 m		31				1.1		
T4-61 m		440	70	175	12	14	9	7.4
T4-152 m		220	133			72		
T5-61 m	130	95	29	20		12	12	
T5-152 m	80	95	124					
Depth (cm)	0-2	0-5	0-5	0-2	0-2	0-2	0-2	0-2

Spatial Disease Patterns

Of the three depths sampled (23, 61, and 137 m), <1% of the fish with fin erosion were collected at 23 m. This is probably a function of low sediment contamination at the shallowest stations (Table 9). Coastal sediments in southern California are

TABLE 10.—Copper, cadmium, and chromium concentrations (ppm dry weight) in surface sediments at the sampling transects from 1975 to 1980. Note that the deeper samples were taken at 152 m while the trawls were made at 137 m. Depth of sediments analyzed at bottom of table. (SCCWRP, unpubl. data.)

	Copper			Cadmium			Chromium		
Station	1975	1978	1980	1975	1978	1980	1975	1978	1980
T0-61 m	48	42		1.7	1.3		137	119	
T0-152 m	66	66		3.3	2.6		170	174	
T1-61 m	362			21			828		
T1-152 m	148			11			317		
T4-61 m	937	427	352	61	28	31	1,480	1,042	972
T4-152 m	555	408		66	24		968	862	
T5-61 m	134	234		8.3	9.2		254	521	
T5-152 m	433	301		41	16		769	605	
Depth (cm)	0-5	0-2	0-2						

TABLE 11.—Mean organic content (percent) of surface sediments at 61 m from 1972 to 1981 and correlation between organic content and years. $\bar{x}$ = mean, SD = one standard deviation, n = sample size, r = correlation coefficient, P = probability that the calculated r came from a population with $\rho = 0$.

Transect	$\bar{x}$	SD	n	r	P
T0	2.13	0.18	13	0.052	0.50
T1	6.83	1.45	17	−0.761	0.001
T4	11.21	1.39	17	−0.831	0.001
T5	7.83	1.62	17	−0.532	0.05

coarser and lower in volatile solids in shallow water, and become finer and higher in volatile solids with increasing depth. Contaminants are generally attached to the finer particles and thus increase in concentration with increasing depth (Hershelman et al. 1982).

The incidence of fin erosion in Dover sole followed the spatial pattern of sediment contaminant distribution. The incidence was highest near the outfalls (44.0% of all Dover sole collected at T4 and 37.3% at T5) and decreased with increasing distance upcoast (20.3% at T1 and 2.0% at T0). The relationship between disease incidence and sediment contaminant levels suggests that fin erosion is the result of contamination and that the incidence of the disease is directly related to the magnitude of contamination. Because preimpact data do not exist, gradients of contamination and disease are assumed not to have existed before sewage discharge began. It is generally accepted that the presence of fin erosion in the environment is the result of contamination (Murchelano and Ziskowski 1976; Sindermann 1979). Controlled laboratory experiments demonstrated that Dover sole exposed to sediments from the Palos Verdes shelf developed fin erosion (Sherwood 1976; Mearns and Sherwood 1977).

Temporal Disease Patterns

The number of species affected by fin erosion declined significantly from 1971 to 1982 and was most rapid from 1971 to 1974 following the wastewater treatment modifications made in the early 1970's. This pattern suggests that the decline was related to reduced surface sediment contamination.

The incidence of fin erosion also declined in two of the three most affected species (Dover and rex soles). The declines were greater at T1 than at T4 or T5; the incidence of the disease at T0, the station farthest from the outfalls, was always low. There was a significant correlation between the sediment concentration of DDT (Table 9) and the proportion of Dover sole with fin erosion (determined by dividing the total number of Dover sole with the disease by the total number of Dover sole collected within a year) at T4-61 m (Spearman $r_s = 0.821, n = 7, 0.02 < P < 0.05$).

The seasonal trends in the catch of Dover sole and the number of Dover sole with fin erosion are the result of recruitment and depth-related migrations. Recruitment occurs at 61 and 137 m, but more fish settle out at 137 m. The magnitude of the seasonal swing appears greater at 61 m where few Dover sole were captured in the first and fourth quarters. Large numbers of Dover sole were collected at 137 m in the fourth quarter but, by the first quarter, the catches had declined substantially. Dover sole apparently move off the shelf into deeper water in the winter and back onto the shelf in the summer. Hagerman (1952) reported an annual depth-related migration of Dover sole into deeper water in the winter related to reproduction and a return migration into shallower water in the summer related to feeding.

Examination of the deseasonalized data revealed that fin erosion declined over the last 4 yr

at the deeper (137 m) stations near the outfalls but not at the depth of the outfalls (61 m). The total catch of Dover sole also declined at 137 m but not at 61 m. The declines in Dover sole abundance in the long-term (1971-82) and deseasonalized quarterly (1979-82) data coincide with declines in surface sediment contamination and therefore are somewhat surprising.

In southern California, Dover sole are an order of magnitude more abundant around the outfalls than in distant control areas. This probably is a function of the distribution of their preferred prey (polychaetes) which are more abundant around the outfalls (Cross et al. in press). Pearcy and Hancock (1978) found a positive correlation between the standing crop of Dover sole and the standing crop of their preferred prey off Oregon. A decrease in the quantity of sewage particles settling at stations distant from the outfalls might cause a reduction in the preferred prey populations accounting for the reduced abundance of Dover sole. The decrease in organic content of surface sediments at T1, and the low value at T0, which was within the 95% confidence interval (2.12-2.84%) for reference areas in northern Santa Monica Bay (Cross, unpubl. data), support this hypothesis.

The trends in fin erosion among calico rockfish were different from those of the two soles. The general increase in disease incidence may result from differential susceptibility.

Effect of Fin Erosion on the Dover Sole Population

Although fin erosion has been reported in fishes from a number of areas around the world [southern California, Puget Sound, and the New York Bight (Sherwood 1982); Japan (Nakai et al. 1973); and northern Europe (Perkins et al. 1972)], no one has yet shown that the disease is harmful to the affected individuals (Murchelano and Ziskowski 1982).

Dover sole recruit to the study area between February and May when they are 40-50 mm SL (Allen and Mearns 1976; Sherwood 1980; Cross unpubl. data). Fin erosion is negligible in new recruits. By the time the fish are 80-100 mm BSL [about 100 d after settlement, based on growth curves presented in Sherwood (1980)], 18% have the disease. The size distributions of Dover sole with fin erosion are narrower than the size distributions of fish without the disease (Fig. 3). Underrepresentation in the lower tail of the size distribution of Dover sole with the disease occurs because the fish do not contract fin erosion until sometime after settlement. Underrepresentation in the upper tail suggests increased mortality among fish with the disease.

A size difference between Dover sole with and without fin erosion was not detected in the data. The χ^2 values increased with successive ages suggesting a significant difference in the size-frequency distributions may occur at an older age. Dover sole older than 7 yr were rarely encountered on the Palos Verdes shelf.

No significant differences were found in the weight-length relationships between males with and without the disease and between females with and without the disease. The significant difference observed between males and females without the disease is characteristic of Dover sole (Hagerman 1952). The lack of significant difference between males and females with fin erosion is difficult to interpret at this time.

Fin erosion appears to have a detrimental effect on the survival rate of Dover sole. Survival rates for Dover sole with and without the disease were similar up to 3 yr of age; thereafter, the survival rate of diseased fish was significantly lower.

CONCLUSIONS

The data presented in this study suggest that 1) fin erosion is the result of exposure to contaminants discharged from the outfalls and 2) the magnitude of disease incidence is directly related to the magnitude of sediment contamination. Disease incidence and sediment contaminant concentrations decrease with increasing distance from the outfalls. Disease incidence is negligible in Dover sole recruits but increases rapidly with increasing body size, and presumably contaminant exposure, after settlement. The number of species affected by the disease, the disease incidence in Dover sole, and the contaminant concentrations of surface sediments have declined over time.

While the prevalence of fin erosion has declined, the disease remains a problem. Fin erosion was observed in 5.9% of the fishes collected at 61 m and 137 m at T4 and T5 in 1982 and appears to affect at least one population causing increased mortalities.

Sindermann (1979) described fin erosion as "Probably the best known but least understood disease of fish from polluted waters..." (p. 719) and concluded "...that generalized disease signs, such

as fin rot... may be characteristic of fishes resident in degraded habitats, where environmental stresses of toxic chemicals, low dissolved oxygen, and high microbial populations exist" (p. 722). The etiology of the disease is unknown. "The multifactorial genesis of disease in marine species is becoming apparent, involving environmental stress, facultative pathogens, resistance of hosts, and latent infections" (Sindermann 1979:741).

ACKNOWLEDGMENTS

I would like to thank the Los Angeles County Sanitation District for providing the monitoring data and Alan Mearns and Leslie Harris for providing the age data on Dover sole. The comments of an anonymous reviewer improved the quality of the manuscript.

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CONFIDENCE LIMITS FOR POPULATION PROJECTIONS WHEN VITAL RATES VARY RANDOMLY

Tim Gerrodette,[1] Daniel Goodman,[2] and Jay Barlow[3]

ABSTRACT

Due to unpredictable future environmental changes, population growth is more realistically viewed as a stochastic than a deterministic process. Environmental variablity is modeled by allowing the population's survival and fecundity rates to be correlated random variables. The expected future population vector and its variance-covariance matrix are computed. The projected total future population size is approximately log-normally distributed, but confidence limits for future population size can be more accurately computed from the distribution of the realized factor of increase. Numerical examples illustrate how the calculation of confidence limits for future population size and of the probability that the population will increase in size can be applied to the management of living resources.

The predicted size of an age-structured population can be projected if its initial size, age distribution, and vital rates are known (e.g., Leslie 1945; Keyfitz 1968). Such population projections are commonly used in fisheries and wildlife management when age-specific fecundity and mortality rates are available. However, there is uncertainty in such projections. First, we rarely know vital rates exactly; rather, we have estimates of the true rates, and these estimates are subject to sampling and other types of errors. Second, the true rates themselves are not constant with time. Environmental conditions are always changing, and the vital rates would be expected to change in response. To an extent, the changes of conditions may themselves be forecast and incorporated into a population model. Some changes, however, are unpredictable, and these changes give rise to fluctuations in the vital rates which make our estimates of population size for some future time less certain. Nevertheless, it may still be possible to make probabilistic predictions about future population size given some statistical knowledge about the fluctuating vital rates.

In this paper we limit ourselves to consideration of the second of these problems, projecting age-structured populations when mortality and fecundity rates vary randomly with time. Recently this topic has been of interest and controversy in a more theoretical context (Boyce 1977; Cohen 1979a, b; Daley 1979; Tuljapurkar and Orzack 1980; Tuljapurkar 1982; Slade and Levenson 1982). In spite of earlier results to the contrary (Boyce 1977), analyses (Sykes 1969; Cohen 1977), and simulations (Slade and Levenson 1982) have shown that when vital rates fluctuate randomly with no serial correlation, the expectation of population size at a future time will be exactly equal to the population size projected using the mean vital rates in a deterministic projection. For application in fisheries and wildlife management, the problem is that the distribution of future population sizes will often be strongly skewed. This skew means that the mean and variance of future population size, even if known, are not sufficient to characterize the distribution and, in particular, not sufficient to compute confidence limits for total population size. In this paper we examine two transformations of this skewed distribution which approximate a normal distribution, and evaluate the accuracy of confidence limits computed from these transformations.

As pointed out by several of the authors cited above and earlier by Lewontin and Cohen (1969) for a non-age-structured population, stochastic effects can cause the modal or most likely population trajectory to decline to extinction, even though the expected or mean population size is growing at a geometric rate. Clearly, if we are to use population projections in fisheries and wildlife management, we should be concerned about the effects of natural variability on the results of our projections. In response to this concern, we have written two com-

[1]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093; present address: Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[2]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093; present address: Department of Biology, Montana State University, Bozeman, MT 59717.

[3]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093; present address: Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted May 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

puter programs for stochastic population projections which can serve as research and management tools. Here we illustrate the utility of these programs with numerical examples, compare our results with recent theoretical analyses, and discuss the implications of these results to the management of living resources.

METHODS

Sykes (1969) presented three models for incorporating stochasticity into population projections. He concluded that the observed variability in human demographic projections was best described by his third model, in which the elements of the Leslie matrix (the effective fecundity rates and the survival rates) are random variables, each with a specified mean and variance, and with specified covariances between them. The model does not allow for serial covariance in vital rates between successive time periods.

Let n_t be a population vector of ω age classes at time t. The stochastic projection model is

$$n_{t+1} = (A + \Delta_t)\, n_t, \qquad t = 0, 1, 2, \ldots$$

where A is a constant projection matrix of mean vital rates and Δ_t is a matrix of random deviations whose elements have a specified covariance structure $\{\mathrm{Cov}(\Delta_i,\Delta_j)\}$ but which are uncorrelated in time. Let $N_t = \sum_{i=1}^{\omega} n_{ti}$ be the total population size at time t. It is convenient to normalize the projected population to the initial population size and consider the distribution of the ratio N_t/N_0. The mean and variance of this ratio are given by

$$E(N_t/N_0) = E(N_t)/N_0 = \sum_{i=1}^{\omega} E(n_{ti})/N_0$$

and

$$\mathrm{Var}\,(N_t/N_0) = \mathrm{Var}\,(N_t)/N_0^2 = \sum_{i=1}^{\omega}\sum_{j=1}^{\omega} \mathrm{Cov}\,(n_{ti},n_{tj})/N_0^2.$$

From Sykes (1969, equations 19 and 20), the mean and variance of the population vector are given by

$$E(n_t) = \{E(n_{ti})\} = A^t n_0$$

and

$$\mathrm{Var}\,(n_t) = \{\mathrm{Cov}\,(n_{ti},n_{tj})\} = \sum_{k=0}^{t-1} A^{t-1-k} \left\{ \sum_{\alpha=1}^{\omega}\sum_{\beta=1}^{\omega} \mathrm{Cov}\,(\Delta_{i\alpha}, \Delta_{j\beta}) \left[\mathrm{Cov}\,(n_{k\alpha},n_{k\beta}) + E(n_{k\alpha})E(n_{k\beta})\right] \right\} A'^{t-1-k}$$

where A' is the transpose of A and where the curly brackets indicate that the expression inside them is the ith element of the vector or the ijth element of the matrix considered.

Tuljapurkar and Orzack (1980) predict that for large t, N_t/N_0 will be lognormally distributed. The mean and variance of the normally distributed variable $\log\,(N_t/N_0)$ are calculated from the mean and variance of the lognormally distributed variable N_t/N_0 by

$$E\,[\log\,(N_t/N_0)] = \log\,[E(N_t/N_0)] - \left\{ \frac{\mathrm{Var}\,[\log\,(N_t/N_0)]}{2} \right\}$$

and

$$\mathrm{Var}\,[\log\,(N_t/N_0)] = \log \left\{ \frac{\mathrm{Var}\,(N_t/N_0)}{[E(N_t/N_0)]^2} + 1 \right\}$$

(Aitchison and Brown 1957). We have found in simulations that the distribution of the realized factor of increase $(N_t/N_0)^{1/t}$ is approximately normal. Based on the assumption that the realized factor of increase is normally distributed, the mean and variance of $(N_t/N_0)^{1/t}$ are computed from the mean variance of N_t/N_0 by methods given in Appendices 1 and 2.

Using the formulae of Sykes (1969), the mean and variance of each age class in the future population can be computed analytically. Confidence intervals for the total population size and for the realized factor of increase, and an estimate of the probability that the future population will be larger than the starting population, are computed based on the assumption that either $\log\,(N_t/N_0)$ or $(N_t/N_0)^{1/t}$ is normally distributed.

We can also simulate the growth of an age-structured population under fluctuating environmental conditions. At each time period, a new set of fecundity and survival rates, the elements of the Leslie matrix, are chosen and used to project the population. Each fecundity and survival rate is a normally distributed random variable with specified mean, variance, and covariance with every other fecundity and survival rate. The projection, starting from the

same initial population vector, may be replicated a given number of times. From these replicated projections, the mean, variance, and covariances of the population vector are computed, together with statistics on a variety of other demographic parameters. The distributions of the final population size and the realized factor of increase are tabulated.

The computer programs to accomplish these stochastic projections are called, respectively, SPP (Stochastic Population Projection) and SLT (Stochastic Life Table simulation). Program listings and guides to the use of both programs are given in Gerrodette et al. (1983). Although lengthy, these programs are suitable for use on many microcomputers.

TABLE 1.—Initial population vector, mean vital rates, and covariance matrix of vital rates for a three age-class population projection. In the covariance matrix, *F* refers to fecundity rate, *P* to survival rate, and numbers to age classes.

Age class	Initial population size	Mean fecundity rate	Mean survival rate	Covariance matrix						
					*F*1	*F*2	*F*3	*P*1	*P*2	*P*3
1	100	0.1	0.7	*F*1	0.0010	0.0020	0.0020	0.0005	0.0005	0.0
2	80	1.0	0.9	*F*2		0.0050	0.0045	0.0010	0.0010	0.0
3	50	0.4	0.0	*F*3			0.0050	0.0010	0.0010	0.0
	230			*P*1				0.0050	0.0045	0.0
				*P*2					0.0050	0.0
				*P*3						0.0

Numerical Examples

Two numerical examples are presented to verify various analytic results and to illustrate the use of programs SPP and SLT in a management context.

The first example is a simple artificial life table with three age classes. The mean vital rates and the covariance matrix for the vital rates are given in Table 1. This example was used to compare the predicted mean and variance in projected population size based on Sykes' (1969) formulae with the actual mean and variance from the simulation. The example was also used to test the assumption that ultimate population sizes will be lognormally distributed, and in particular whether accurate confidence limits for the tails of the distribution can be made based on this assumption.

The second example is based on a real population. A northern fur seal, *Callorhinus ursinus*, population is projected using vital rates consistent with a phase of rapid growth which occurred earlier in this century. The mean vital rates which govern the dynamics of the population are given in Table 2 (taken from Goodman 1981: table 1) and confer a population growth rate of about 8% per year. The initial age vector in this case was chosen to be the stable age distribution with a total of 100,000 females. Values for the standard deviations in vital rates in Table 2 were selected by choosing reasonable values for their coefficients of variation. Correlations in vital rates were assumed to be 0.9 between fecundities at different ages, 0.9 between survival rates at different ages, and 0.5 between all fecundities and survival rates.

TABLE 2.—Initial population vector, means, and standard deviations (S.D.) of vital rates for a fur seal population projection used as a numerical example in the text. Mean rates are taken from Goodman (1981: table 1). Each age class represents 1 yr, and only the female portion of the population is tabulated. The initial population vector is in the stable age distribution with a total of 100,000 females.

Age class	Initial population size	Mean fecundity rate	S.D.	Mean survival rate	S.D.
1	17,618	0.0000	0.0000	0.8786	0.0439
2	14,312	0.0000	0.0000	0.8786	0.0439
3	11,627	0.0050	0.0003	0.8837	0.0442
4	9,500	0.0151	0.0008	0.8888	0.0444
5	7,807	0.2631	0.0132	0.9039	0.0090
6	6,525	0.3693	0.0185	0.9191	0.0092
7	5,545	0.4250	0.0213	0.9342	0.0093
8	4,789	0.4604	0.0230	0.9443	0.0094
9	4,182	0.4756	0.0238	0.9494	0.0095
10	3,671	0.4705	0.0235	0.9443	0.0094
11	3,205	0.4655	0.0233	0.9292	0.0093
12	2,753	0.4554	0.0228	0.9039	0.0090
13	2,301	0.4402	0.0220	0.8786	0.0088
14	1,869	0.4250	0.0213	0.8484	0.0085
15	1,466	0.4048	0.0202	0.8029	0.0080
16	1,089	0.3794	0.0190	0.7524	0.0075
17	757	0.3542	0.0177	0.6918	0.0069
18	484	0.3187	0.0159	0.6262	0.0063
19	280	0.2833	0.0142	0.5454	0.0055
20	141	0.2479	0.0124	0.4494	0.0045
21	59	0.2024	0.0101	0.3282	0.0033
22	18	0.1467	0.0073	0.1009	0.0010
23	2	0.0657	0.0033	0.0000	0.0000
Total	100,000				

RESULTS

Example 1.

The results of the stochastic projection by program SPP are presented in Table 3. The second column shows the expected (mean) population vector for each time step. The mean population vector is obtained by projecting with the mean vital rates. The covariance matrix for the population vector gives, on the diagonal, the variances of each age class and, above the diagonal, the covariances between age classes.

The calculations using Sykes' formulae concur with the results of the Monte Carlo simulation of a stochastic population projection, taking the entries of the life table as time-varying random variables (program SLT). In Tables 4 and 5 the results of the simulation are presented. The means and covariances of the vital rates actually achieved on this particular run of program SLT are shown in Table 4 and are close to the specified rates given in Table 1. By comparing the results in Table 5 with those of time step 6 in Table 3, we see that the results of the simulation (SLT) and the analytic solution (SPP) agree closely.

The distribution of the ratio of the final population size to the initial population size is shown as a histogram in Figure 1A. The curve is skewed to the right,

TABLE 3.—Results of the stochastic projection of the population, given in Table 1, through 6 time steps (program SPP). The columns labeled "95% C.L." give the lower and upper 95% confidence limits for total population size and for the realized factor of increase relative to the initial population. The last column gives the probability *P* that the final population size will be greater than the initial population size.

Time step	Expected population vector	Covariance matrix			Total population Mean	Total population Lower 95% C.L. / Upper 95% C.L.	Factor of increase Mean	Factor of increase Lower 95% C.L. / Upper 95% C.L.	*P*
	100								
0	80				230				
	50								
	110	142.5	18.0	14.4		215		0.934	
1	70		50.0	36.0	252	289	1.096	1.258	0.8764
	72			32.0					
	110	261.5	48.4	73.5		197		0.925	
2	77		131.0	46.1	250	307	1.041	1.156	0.7545
	63			65.3					
	113	365.3	94.4	154.1		193		0.934	
3	77		189.7	68.7	259	335	1.039	1.134	0.7856
	69			136.4					
	116	485.5	158.2	219.9		187		0.950	
4	79		244.9	99.0	264	356	1.033	1.116	0.7808
	69			184.2					
	119	559.6	230.8	287.1		184		0.957	
5	81		307.5	141.7	271	378	1.031	1.105	0.7910
	71			231.0					
	121	736.2	309.8	366.2		182		0.961	
6	83		367.0	189.7	277	400	1.029	1.096	0.7990
	73			283.5					

TABLE 4.—Means, variances, and covariances of vital rates achieved during a Monte Carlo projection of the population given in Table 1 (program SLT). Values were computed on the basis of 30,000 vectors of vital rates. *F* refers to fecundity rate, *P* to survival rate, and numbers to age classes. Values in this table should be compared with the "target" values in Table 1.

	Mean	Covariance matrix *F*1	*F*2	*F*3	*P*1	*P*2	*P*3
*F*1	0.10016	0.00101	0.00202	0.00201	0.00049	0.00045	0.0000
*F*2	1.00027		0.00505	0.00453	0.00100	0.00092	0.0000
*F*3	0.39998			0.00502	0.00099	0.00091	0.0000
*P*1	0.69992				0.00501	0.00414	0.0000
*P*2	0.89744					0.00435	0.0000
*P*3	0.00000						0.0000

TABLE 5.—Results of the Monte Carlo simulation of the 6 time-step projection of the population whose age structure and vital rates are given in Table 1 (program SLT). Sample size for the simulation was 5,000 trials. Results in this table should be compared with the "predicted" values in the last row of Table 3. Here P is the proportion of final population sizes greater than the initial population size.

Time step	Mean population vector	Covariance matrix			Mean total population	Mean factor of increase	P
	121	741.3	314.7	369.8			
6	83		371.7	187.6	277	1.029	0.7954
	73			281.5			

as anticipated. Both the logarithmic transformation (Fig. 1B) and the root transformation (Fig. 1C) appear to normalize the distribution. When the cumulative frequency distributions are plotted on normal probability scales (dots in Fig. 1), however, the root transformation appears superior to the logarithmic. The dots in Figure 1C are nearly linear, indicating that the distribution is close to normal.

In Table 6 the accuracy of the 95% confidence limits for the total population size computed by the logarithmic and root transformations is compared for projections of 2, 5, and 10 time steps, using the same numerical example. Program SLT calculates the proportion of final populations which fall above and below the computed upper and lower confidence limits. We expect that 2.5% of the cases should fall above the upper limit and 2.5% below the lower limit if the 95% confidence interval has been correctly estimated. Table 6 shows that both the logarithmic and the root transformations do a fair job of estimating the 95% confidence limits. The root transformation, however, appears more accurate in this example, as well as in other examples we have tried, when the number of time steps is small. When the number of time steps is large (50-100), both transformations produce normally distributed variables.

Since the root transformation gave the most accurate results for short projections, we used this transformation in program SPP to compute a confidence interval on total population size. More details of the

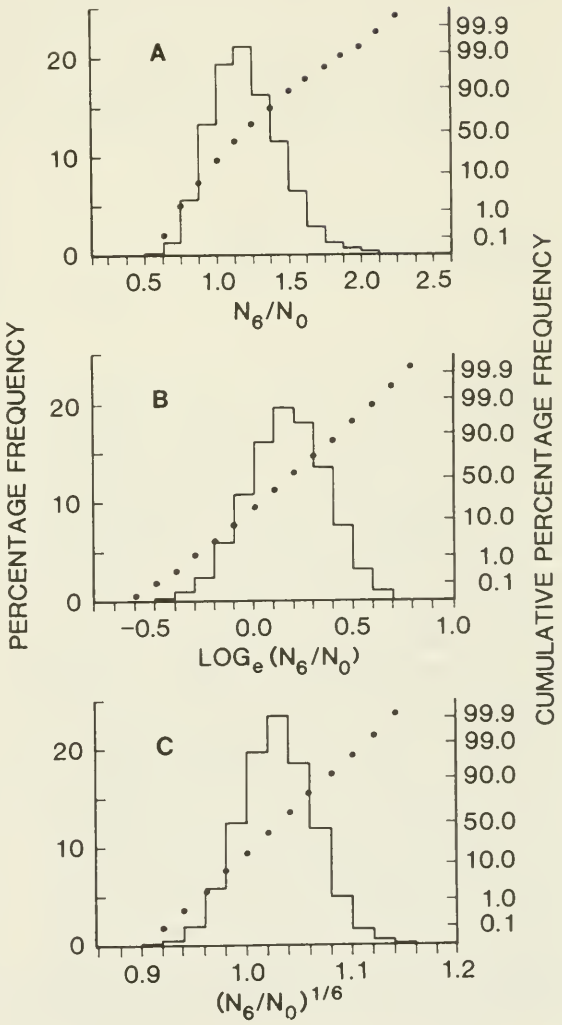

FIGURE 1.—Distributions of future total population size under variable conditions. Histograms show the percentage frequency, and dots the cumulative percentage frequency plotted on a normal probability scale, for 5,000 stochastic projections of the population given in Table 1 for six time steps. A. Distribution of N_6/N_0, the final population size divided by the initial. B. Distribution of $\log_e (N_6/N_0)$. C. Distribution of $(N_6/N_0)^{1/6}$, the realized factor of increase.

TABLE 6.—Accuracy of the 95% confidence limits (C.L.) on population size estimated by the logarithmic and root transformations of the distribution of total population size. For each transformation, the estimated lower and upper confidence limits are shown for projections of the population given in Table 1 for 2, 5, and 10 time steps. The columns labeled "Proportion beyond C.L." give the actual proportion of 10,000 stochastic projections using program SLT which fall below the estimated lower limit and above the estimated upper limit for each transformation. Each set of projections was replicated 3 times. The root transformation estimates the 95% confidence interval on population size more accurately, especially for short projections.

No. of time steps to projection		Transformation			
		Logarithmic		Root	
		Estimated 95% C.L.	Proportion beyond C.L.	Estimated 95% C.L.	Proportion beyond C.L.
2	Lower	199	0.0311	197	0.0256
			0.0317		0.0255
			0.0295		0.0231
	Upper	309	0.0160	307	0.0204
			0.0181		0.0214
			0.0199		0.0228
5	Lower	187	0.0290	184	0.0251
			0.0285		0.0242
			0.0318		0.0260
	Upper	380	0.0227	378	0.0245
			0.0219		0.0235
			0.0215		0.0235
10	Lower	178	0.0266	175	0.0238
			0.0280		0.0252
			0.0286		0.0257
	Upper	489	0.0226	486	0.0234
			0.0211		0.0221
			0.0217		0.0226

example projection are shown in the columns on the right side of Table 3. The mean and the 95% confidence interval for the total population size and for the realized factor of increase are given for each time step. As the population vector approaches the stable age distribution, the ratio between successive mean total population sizes approaches the asymptotic value 1.0240. The mean realized factor of increase shown in Table 3, which is computed relative to the initial population, does not converge on this asymptotic value; nor can the mean realized factor of increase be computed from the ratio of the mean final population size to the initial population size. Instead, the mean and variance of the realized factor of increase are computed by methods described above.

The probability that the total population size will have increased over its initial value is also shown for each time step in the last column of Table 3. In this particular example, since we did not begin with the stable age distribution, this probability decreases at first and then increases. As a further check, program SLT computes the proportion of cases in which the final population was greater than the initial population, and this answer (0.7954, Table 5) is close to the probability computed analytically by program SPP assuming that the realized factor of increase is normally distributed (0.7990, Table 3). Given a population whose age structure and dynamics conform to the values given in Table 1, therefore, we can make the statement that there is an 80% chance that the population will be larger 6 time steps from now and a 20% chance that it will be smaller.

Example 2.

The results of the stochastic projection of the northern fur seal population by program SPP are given in Table 7 and Figure 2. Table 7 shows that after 5 yr, the expected (mean) number of 9-yr-olds, for example, is 6,188 with a standard deviation of 333. The expected total population size is 147,982 with a standard deviation of 8,832. The mean and standard deviation of the realized factor of increase are 1.0812 and 0.0129, respectively; from these values we compute the 99% confidence interval on population size to be from 126,410 to 171,930. Note

TABLE 7.—Results of the 5-yr stochastic projection of the northern fur seal population, based on the age structure and vital rates given in Table 2. Probability that the final population > initial population = 0.999+.

Age class	Expected population size	Standard deviation
1	26,071	1,672
2	21,179	1,619
3	17,205	1,519
4	14,058	1,402
5	11,553	1,280
6	9,655	972
7	8,205	720
8	7,087	516
9	6,188	333
10	5,432	121
11	4,743	106
12	4,075	92
13	3,406	76
14	2,767	62
15	2,170	49
16	1,611	36
17	1,121	25
18	717	16
19	415	9
20	209	5
21	87	2
22	26	1
23	2	0.05
Total	147,982	

	Total population	Factor of increase
Lower 99% C.L.	126,410	1.0480
Expected value (mean)	147,982	1.0812
Upper 99% C.L.	171,930	1.1145

that, as will generally be the case, the confidence interval for total population size is not symmetric about the mean value.

In the last line of Table 7, the probability of an increased population is shown to be very close to 1.0. In other words, it is virtually certain that the population will have increased in size after 5 yr. Figure 2 presents the results for total population size graphically. The 95% and 99% confidence limits computed by program SPP are shown for each time step. The confidence limits grow nearly geometrically.

DISCUSSION

Fishery and wildlife management often involves predictions of population size, and, owing to imperfect knowledge of the world, these predictions are uncertain. Accordingly, a practical analysis attaches estimates of confidence intervals for any given prediction. The programs described in this paper carry out the computation of confidence intervals for projections of age-structured populations, if we can specify the statistics of the variation in the age-specific vital rates. Realistically, we do not expect there to be be many examples where the statistics of the variation in vital rates are genuinely known with substantial precision, for these rates are difficult to measure in natural populations. Nevertheless, in an imperfect world, management decisions must be made with imperfect data. A considerable component of the uncertainty in a population prediction will be owing to the phenomena treated in this paper. Thus, even the use of very rough guesses at the statistics of the variation in the age-specific vital rates, in order to estimate confidence intervals in a population projection, is preferable to neglecting this source of variation entirely. At the very least, incorporation of speculative estimates in this applied context will allow the exploration of "what if" questions in a fashion that can indicate priorities for future data gathering.

In many fish and aquatic invertebrate species, there is an enormous variation in the success of year classes. In such cases the population dynamics may be dominated by the overwhelming abundance of one

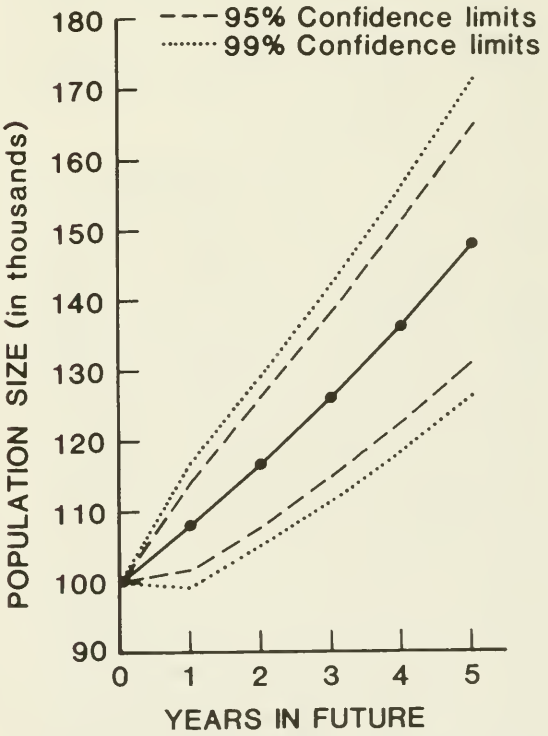

FIGURE 2.—Confidence limits for future total female population size for the northern fur seal, based on the schedule of vital rates in Table 2. The solid line plots the mean population trajectory.

or two cohorts. The environmental factors which lead to such huge variations in recruitment are as yet imperfectly understood for most species. In order to predict future population sizes, the year-to-year variation could be incorporated into the variances of the effective fecundity terms in the first row of the Leslie matrix. This will lead to enormous (but realistic) confidence limits for predicted future population sizes of such stocks. A more fruitful use of the results of this paper, however, would be to separate recruitment uncertainty from survival uncertainty and to calculate a confidence interval on future population size given recruitment success for a particular cohort. Among harvested species such a conditional forecast could be used to incorporate environmental variation into management recommendations.

In keeping with the fact that applied management may often depend on very elementary quantities, we also calculate a particularly important special statistic of the distribution of projections – the probability that the population will increase under the specified conditions. In the first example, the probability of an increased population was found to be about 0.8. In the second example, the fur seal population projection, there is a higher probability that the population will increase. Starting with the female population of 100,000, the calculations indicate 99% certainty that the population will have increased to between 126,410 and 171,930 in 5 yr.

Our simulations of stochastic population growth differ from previous efforts by Boyce (1977) and Slade and Levenson (1982) by allowing all vital rates to vary simultaneously, rather than only one at a time, and by permitting correlations among the vital rates to be specified. In the stochastic growth models of Cohen (1977, 1979a) and Tuljapurkar and Orzack (1980), at each time step the population finds itself in one of several possible environments. Within each environment vital rates are fixed. By contrast, here we model a single variable environment whose conditions, as reflected in the population's vital rates at any point in time, are never precisely duplicated. The results of Example 1 verify the results for the mean and variance of future population vectors and show that the mean and variance for total ultimate population size can be computed from Sykes' formulae. Our results confirm the conclusions of Cohen (1977), Tuljapurkar and Orzack (1980), and Slade and Levenson (1982) that the expected mean value of a stochastic population projection with no serial correlation in vital rates is equivalent to the value projected deterministically from mean vital rates. Cohen (1979a, b) and Tuljapurkar (1982) address the more general question of serial correlation in vital rates.

All of the work cited above has been concerned with the state of the population at a time in the future much greater than will generally be useful in management. In this paper we have examined the stochastic behavior of the population at a shorter time in the future. Example 1 has verified that the distribution of ultimate population sizes from stochastic population projections is approximately lognormal (Tuljapurkar and Orzack 1980). From the perspective of fitting the tails of this distribution for a small number of time steps t, however, it appears better to assume that the $1/t$th power of the distribution is normally distributed. In either case the distribution of ultimate population sizes is skewed (with long tails at the higher values), and the skew becomes more pronounced as t increases. An important property of such a distribution is that the most likely or modal population value will always be smaller than the mean. How much smaller depends on the number of time steps t, and on the variances and covariances among the survival and fecundity rates.

An interesting theoretical and practical problem is to find a descriptor of population growth under stochastic conditions which characterizes the skewed distribution of ultimate population size. Cohen (1979a) has proposed two measures of long-run population growth: λ, the ensemble average of realized factors of increase; and μ, the factor of increase needed to realize the ensemble average of final population sizes. The first is a measure based on growth rates, while the second is based on population sizes (Cohen 1979b). The average realized factor of increase calculated here is analogous to λ. If the Leslie matrix of mean vital rates is known, μ is easily calculated as the dominant eigenvalue of that matrix. The problem, as we have seen, is that under stochastic conditions the mean of the population sizes is not very informative and may, in fact, be misleading. Tuljapurkar (1982) has proposed a growth measure α which leads to the approximate median population size. The two measures proposed here – namely, $E[(N_t/N_0)^{1/t}]$ and $E[\log(N_t/N_0)]$ – are close approximations to the rate of growth leading to the modal population size. As such, they may loosely be said to describe the most probable trajectory of the population under stochastic conditions.

ACKNOWLEDGMENTS

The work was supported by a National Research Council Fellowship to the first author and by NOAA

Contract 80-ABC-00207 to the second. We thank Douglas Chapman for his helpful comments. Typing assistance was provided by Lorraine Prescott and her staff at the Southwest Fisheries Center.

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APPENDIX 1.

Calculation of the mean and variance of the realized factor of increase, assuming it is normally distributed.

Let λ, the realized factor of increase, be defined as the tth root of the ratio of the population size at time t to the initial population size:

$$\lambda = \left(\frac{N_t}{N_0}\right)^{1/t}$$

or

$$\lambda^t = \frac{N_t}{N_0}$$

Let μ be the mean and ν the variance of λ. The mean and variance of λ^t are given by formulae in the Methods section. The problem is to find the mean and variance of λ.

Let $F(\mu,\nu)$ be a function which gives the tth moment of λ:

$$F(\mu,\nu) = E(\lambda^t).$$

Similarly let $G(\mu,\nu)$ be a function which gives the variance of λ^t in terms of the tth and $2t$th moments of λ:

$$G(\mu,\nu) = E(\lambda^{2t}) - [E(\lambda^t)]^2.$$

Now assume that λ is normally distributed. Appendix 2 gives a recursive algorithm which allows any moment of a normally distributed variate to be calculated. From the tth and $2t$th moments of λ, the functions F and G can be computed from the equations above. Generally, F and G will be tth and $2t$th order polynomials in μ and ν. Then, with F and G known, we have a system of two equations

$$F(\mu,\nu) - E(\lambda^t) = 0$$
$$G(\mu,\nu) - \mathrm{Var}(\lambda^t) = 0$$

in two unknowns. Given initial estimates of μ and ν, a two-variable version of Newton's method, or any similar iterative technique, can be used to converge on a simultaneous solution.

APPENDIX 2.

A recursive algorithm for computing the higher order moments of the normal distribution.

The moment generating function for the normal distribution is

$$M_x(t) = e^{\mu t + \frac{\nu t^2}{2}}$$

where μ is the mean and ν is the variance of the normal variate x. The nth moment of x is found by evaluating, at $t = 0$, the nth derivative of $M_x(t)$ with respect to t. The nth differentiation with respect to t leads to the series

$$(\mu + \nu t)^n M_x(t) + \ldots + A(\mu + \nu t)^\alpha \nu^\beta M_x(t) + B(\mu + \nu t)^{\alpha-2} \nu^{\beta+1} M_x(t) + \ldots,$$

which, evaluated at $t = 0$, gives

$$\mu^n + \ldots + A\mu^\alpha \nu^\beta + B\mu^{\alpha-2} \nu^{\beta+1} + \ldots,$$

where A and B are coefficients and α and β are exponents such that $\alpha + 2\beta = n$. The next [$(n + 1)$th] differentiation of the middle terms gives

$$\begin{aligned} &A(\mu + \nu t)^{\alpha+1} \nu^\beta M_x(t) + A\alpha(\mu + \nu t)^{\alpha-1} \nu^{\beta+1} M_x(t) \\ &+ B(\mu + \nu t)^{\alpha-1} \nu^{\beta+1} M_x(t) + B(\alpha - 2)(\mu + \nu t)^{\alpha-3} \nu^{\beta+2} M_x(t) \\ &= \ldots + (A\alpha + B)(\mu + \nu t)^{\alpha-1} \nu^{\beta+1} M_x(t) + \ldots \end{aligned}$$

which, evaluated at $t = 0$, gives

$$\ldots + (A\alpha + B)\mu^{\alpha-1} \nu^{\beta+1} + \ldots.$$

Thus the coefficient of each term of the series of the $(n + 1)$th moment can be computed from the two terms in the series of the nth moment "before" and "after" it. The exponents of μ and ν follow the regular pattern shown.

LIFE HISTORY CHARACTERISTICS OF *PANDALUS MONTAGUI* AND *DICHELOPANDALUS LEPTOCERUS* IN PENOBSCOT BAY, MAINE

David K. Stevenson[1] and Fran Pierce[2]

ABSTRACT

A number of life history characteristics of two species of pandalid shrimp from Penobscot Bay, ME, were inferred from length-frequency and relative abundance data collected on five occasions during a bottom trawl survey in 1980-81. *Pandalus montagui* is a sequential hermaphrodite. Sex transition occurs throughout the year, but most transitional individuals were observed in late March. Most individuals change sex shortly before or after reaching age 2, but some do so either a year earlier or a year later. Ovigerous females were observed from late November through January; eggs are apparently produced during the second, third, and fourth years. Fifteen percent of the 0 age-group caught in the fall of 1980 were females which may never have functioned as males. Growth was rapid in the spring and summer and negligible in the late fall and winter. Females which changed sex at age 1 were larger than females which changed sex a year later. *Dichelopandalus leptocerus* is not hermaphroditic. Ovigerous females were collected primarily in late November and early December. Some females produce eggs during their first and second years, but most do so only during their second year. None of the females caught during this study appeared to be older than age 2; a few large males remained in the population during their third year of life. Females of both species were larger than males of the same age-group, a distinction which was attributed to differences in growth rate and, for *P. montagui*, was associated with earlier sex transition. Larger shrimp of both species migrated down the Bay into deeper water as the winter progressed.

The Pandalidae are a family of boreal, subarctic shrimp composed of 2 genera and about 20 species. Four species (*Pandalus borealis*, *P. montagui*, *P. propinquus*, and *Dichelopandalus leptocerus*) are common in offshore waters of the Gulf of Maine (Wigley 1960). Of these, *P. borealis* is the largest, reaching a maximum total length of 17-18 cm (7 in), and has been the object of a directed winter fishery in coastal waters of the Gulf of Maine since the late 1930s (Scattergood 1952) and in coastal and offshore waters since 1958[3]. This species is also exploited commercially on the west coast of North America, in the Canadian Maritime Provinces, on the west coast of Greenland, in the Norwegian and North Seas, and in the northwest Pacific (Balsiger 1981).

Pandalus montagui and *D. leptocerus* are smaller species (maximum length 10 cm or 4 in), which are harvested incidentally with *P. borealis* in the Gulf of Maine, but have little or no market value because of their size. *Pandalus montagui* is also harvested as an incidental species in the Gulf of St. Lawrence (Balsiger 1981), and for many years was the object of several localized commercial beam trawl fisheries in the southern North Sea and in Morecambe Bay, northwest England, until declining stock sizes led to the demise of the fisheries in the Thames estuary (described by Mistakidis 1957) and Morecambe Bay in the 1950s and 1960s. Warren (1973) described a fishery for *P. montagui* in the Wash on the east coast of England which was still active in the early 1970s. *Pandalus propinquus* is also smaller than *P. borealis* and is generally restricted to deeper water (165-330 m in New England waters according to Wigley 1960); consequently it is rarely taken in Gulf of Maine commercial catches.

Pandalus montagui is differentiated taxonomically into two subspecies: *P. montagui tridens* in the North Pacific and *P. montagui montagui* in the North Atlantic from the Arctic south to the British Isles and Cape Cod (Simpson et al. 1970) or Rhode Island (Rathbun 1929). According to Simpson et al. *P. montagui montagui* is found in estuaries, coastal waters, and offshore in depths of 5 to over 700 m, but is more common in shallow waters (20-90 m); at depths > 90 m it is gradually replaced by *P. borealis*.

[1]Zoology Department, University of Maine, Orono, ME 04469 and Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

[2]Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

[3]Stickney, A. P. 1980. A characterization of the northern shrimp fishery of Maine. *In* C. J. Walton (editor), Fisheries management and development, Vol. III, Element D: Characterization of the shellfisheries, p. 244-293. Completion report to the State Planning Office, Oct. 1, 1978-Sept. 30, 1979, Maine Department of Marine Resources, Augusta.

Manuscript accepted August 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

Squires (1968) reported that *P. borealis* occurred together with *P. montagui* in depths < 200 m in the Gulf of St. Lawrence and southwest of Newfoundland, but at depths between 200 and 300 m with a smooth detritus bottom and temperatures of 4°-6°C, only *P. borealis* were caught; in colder temperatures (−1° to 3°C) in this same depth range, *P. montagui* were more abundant. *Pandalus montagui* was described as a more eurythermal and eurybathic species than *P. borealis*. Of all the pandalids in the northwest Atlantic, *P. montagui* is the only one which inhabits colder Arctic waters < 1.5°C (Squires 1966). The Atlantic subspecies of *P. montagui* has been the subject of several biological studies (Mistakidis 1957; Allen 1963; Couture and Trudel 1969a, b).

Dichelopandalus leptocerus is distributed in the northwest Atlantic from Newfoundland to North Carolina (Rathbun 1929). It has not been reported from the northeast Atlantic and is rare in the northern Pacific (Squires 1966). During a November 1956 bottom trawl survey in New England waters, *D. leptocerus* was much more widely distributed than *P. montagui* or *P. borealis* (Wigley 1960). *Dichelopandalus leptocerus* was also found over a broad depth range (33-340 m), but was common between 35 and 145 m and at temperatures (in November) of 5°-20°C, whereas *P. montagui* occurred primarily between 70 and 135 m and at temperatures of 6°-10°C. *Dichelopandalus leptocerus* was also collected in areas where bottom sediments contained low, medium, and high quantities of organic matter, whereas *P. montagui* appeared to be associated with sediments with relatively low organic content. Thus, in several ways, *D. leptocerus* appears to have less restricted habitat requirements than *P. montagui* (or *P. borealis*). No detailed biological studies of *D. leptocerus* have been published.

The Maine Department of Marine Resources conducted an exploratory bottom trawl survey to determine the abundance and distribution of pandalid shrimp populations in Penobscot Bay (Figure. 1) during 1980-81. During the course of this survey, biological data were collected from about 10,000 shrimp. The objective of this paper is to describe important life history characteristics of *P. montagui* and *D. leptocerus* in Penobscot Bay (the Bay); these include breeding seasons, female sizes and ages at maturity, sex transition, growth, longevity, and migratory behavior. Aspects of the life cycle and reproductive biology of each species were examined as functions of time of year, depth, and location within the Bay.

METHODS

The survey was conducted over the course of a 12-mo period from late November 1980 to early October 1981. Samples were collected during five distinct periods of time at 19 different stations located from Cape Jellison in the northern end of Penobscot Bay to Mark Island, a distance of about 37 km (23 mi) (Fig. 1). Stations were established at depths ranging from 12 m (40 ft) to 84 m (280 ft) and were located in areas of trawlable bottom. Since a primary objective of the survey was to stimulate commercial shrimp fishing, no attempt was made to randomly select station locations, depths, or sampling times. Attempts were made, however, to return to each station as often as possible so as to determine the seasonal variation in the relative abundance of different sexes, reproductive stages, and size groups of each species at individual locations over the course of the year. Adjacent, well-defined, length groups were assumed to represent successive age-groups.

A total of 45 successful tows (i.e., tows that were not aborted because of bottom obstructions, damage to the trawl, or gear malfunction) were made during the entire survey. Of these, 37 tows which could be assigned to a specific area, depth range, and sampling period were selected for data analysis. Area 1 was defined as the upper Bay, area 2 as west of Islesboro, area 3 as south of Islesboro, and area 4 as east of Islesboro; depth ranges were defined as shallow (12-25 m), moderate (25-50 m), and deep (50-85 m) (Table 1). The distributions of sampling effort between stations by sampling period, area, and depth range are shown in Table 2. No data were

TABLE 1.—Definitions of coded sampling periods, areas, and depth ranges, 1980-81 Penobscot Bay shrimp survey.

Sampling periods	
1	20 November-2 December 1980
2	21-29 January 1981
3	24-31 March 1981
4	16 July-18 September 1981
5	5-6 October 1981
Areas	
1	Upper Bay: stations 2, 3, 4, 6, 18
2	West of Islesboro: stations 1, 5, 9, 10, 14
3	South of Islesboro: stations 7, 8, 12, 15, 16, 17, 19
4	East of Islesboro: stations 11, 13
Depth ranges	
1	12-15 m (shallow)
2	25-50 m (moderate)
3	50-85 m (deep)

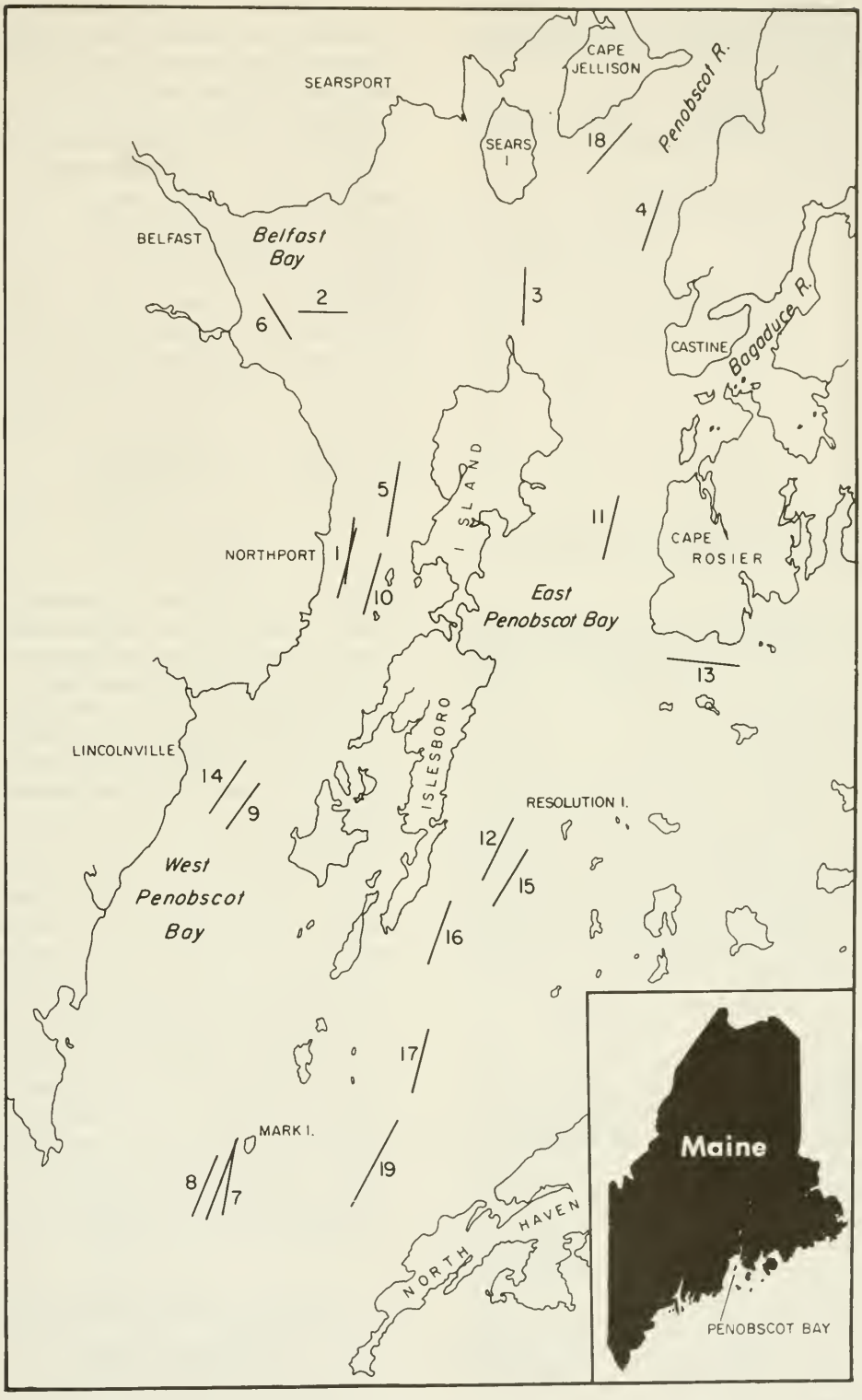


FIGURE 1.—Map of Penobscot Bay, ME, showing bottom trawl stations visited during 1980-81 survey.

TABLE 2.—Distribution of sampling effort (number of tows per station) by sampling period, area, and depth range, 1980-81 Penobscot Bay shrimp survey.[1]

	Sampling period					Area				Depth		
Station	1	2	3	4	5	1	2	3	4	1	2	3
1	2	1		6			9				9	
3	1		1			2				2		
4	1					1				1		
5	1						1				1	
6	1					1				1		
7		1	1		1			3				3
8	1							1				1
9	1		1				2				1	1
10	1	1	3				5				5	
11			1		1				2		1	1
12		1						1				1
13		1							1			1
15		1						1				1
16		1	1		1			3				3
17		1						1				1
18		2				2				2		
19			1					1				1
Totals	9	10	9	6	3	6	17	11	3	6	17	14

[1]See Table 1 for definitions of coded sampling periods, areas, and depth ranges.

available from stations 2 and 14. Trawling operations were limited to the area between Northport and Islesboro in the summer of 1981, since the only vessel available at that time was not equipped to work elsewhere in the Bay.

The trawl used was a semiballoon shrimp try-net with a 7.6 m (25 ft) headrope and 9.5 m (31 ft) footrope with no rollers; mesh size was 38 mm (1½ in) in the body and 31 mm (1¼ in) in the cod end. The trawl was also equipped with a 12.5 mm (½ in) liner. The net was rigged on 1.2 m (4 ft) legs with ark floats on the headrope and 2/0 chain on the footrope. The trawl doors were hardwood, 76 × 41 cm (30 × 16 in), with iron bracings and a wide shoe. The net was fished on a single trawl wire attached to a 30.5 m (100 ft) wire net bridle. All tows lasted 30 min and were made at speeds varying from 1.5 to 2.5 kn. Loran bearings were recorded at the beginning and end of each tow, and depth was recorded either as a single reading or at the beginning and end of each tow. Location and depth could not be determined in the summer since the vessel used then did not have sonar or navigational equipment. Although three different vessels were used during the course of the survey, the gear was identical and was fished the same way during the entire survey.

If catches were small (under 1 kg), the entire catch was generally brought to the laboratory and frozen for later analysis; otherwise, the catch was subsampled aboard the vessel. In some cases, large samples were further subsampled in the laboratory after they were thawed. Inasmuch as was possible, all samples and subsamples were randomly selected. Samples (or subsamples) of 200-900 g were sorted (after removing extraneous "trash") by species according to morphological characteristics described by Rathbun (1929). Biological data were compiled for a total of 7,259 *D. leptocerus* and 2,475 *P. montagui*; numbers of *P. borealis* were inadequate for data analysis. Each individual shrimp was sexed (male, female, or transitional) using external morphological characteristics for the genus *Pandalus* originally described by Wollebaek (1908), Berkeley (1930), Jägersten (1936), and Leloup (1936) and summarized by Mistakidis (1957). The females were further grouped as ovigerous or non-ovigerous depending on whether or not the eggs had "dropped" and were being carried on the pleopods; the non-ovigerous females were further subdivided into two groups—those which had never carried eggs before and those which had—based on the presence or absence of sternal spines. This characteristic of non-ovigerous females was originally described by McCrary (1971) for three pandalid species (*Pandalus borealis*, *P. goniurus*, and *P. hypsinotus*) in Alaska. Stage I females were defined as those which had not carried eggs before and Stage II females as those which had; there was no way to distinguish between females which had carried eggs only once before and those which had carried eggs more than once. Carapace lengths were measured between the eye socket and posterior dorsal edge of the carapace and recorded to the nearest 0.1 mm.

For each species, the numbers and lengths of shrimp in each biological category (sex, with or without eggs, Stage I or II) were compiled by sampling period, geographic area, and depth range. Length frequencies were expressed as numbers of shrimp per 0.5 mm dorsal carapace length. Since nearly all of the samples collected in areas 1-3 were also collected in specific depth ranges (i.e., all 6 samples from area 1 were from shallow water, 16/17 samples from area 2 were from moderate depths, and all samples from area 3 were from deep water), length frequencies were presented for appropriate area/depth combinations. Length-frequency data for *P. montagui* collected in October 1981 were not presented since so few individuals were captured.

RESULTS AND DISCUSSION

Breeding Seasons and Female Sizes (Ages) at Maturity[4]

Nearly all the ovigerous female *D. leptocerus* were

caught in November-December 1980 (Table 3), although a few remained in January and March. It was therefore apparent that most eggs hatched during a relatively short period of time in late December and early January. Although only the larger size group was carrying eggs (Fig. 2D), the presence of a few Stage II non-ovigerous females in roughly the same size range (Fig. 2C) indicated that some females produced eggs a year earlier as well. It could not be determined from the samples collected during this study whether the younger females spawned earlier or later than the older group. The fact that so few Stage II females were captured in the Bay at any time of year indicated that most of the spawning population was made up of first time spawners. Ovigerous females were collected at all depths and in all areas (Tables 4, 5), but made up a greater percentage of the catch at moderate depths in area 2.

Nearly all of the ovigerous female *P. montagui* were collected in November-December and late January (Table 6); the fact that 50% of the females in late January were still ovigerous suggests that eggs hatched over a more prolonged period then was true for *D. leptocerus*, possibly from November at least through February. Females belonging to two North Sea *P. montagui* populations were reported to carry eggs primarily between November and February (Mistakidis 1957; Allen 1963), although ovigerous females were observed from mid-October to April in the Thames estuary by Mistakidis. Hatching times were reported for the same populations as late February through April with peak activity in April. According to Couture and Trudel (1969b), ovigerous females were observed in Grand-Rivière, Quebec, beginning in July and accounted for the greatest percentage of the population in October (no samples

TABLE 3.—Percent total number of male and female *Dichelopandalus leptocerus* collected at all locations and depths in Penobscot Bay during five sampling periods in 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	11/20-12/2 1980	1/21-1/29 1981	3/24-3/31 1981	7/16-9/18 1981	10/5-10/6 1981	Total
Total males	49.7	65.3	59.4	47.6	53.0	53.2
Females/Stage I	32.0	33.5	37.8	50.2	45.3	38.8
Females/Stage II	1.4	0.3	1.5	2.2	1.5	1.5
Total non-ovigerous females	33.4	33.7	39.3	52.4	46.8	40.2
Ovigerous females	16.8	1.0	1.3	0.0	0.2	6.6
Total females	50.3	34.7	40.6	52.4	47.0	46.8
Total no. individuals	2,694	729	1,151	1,107	1,577	7,259

TABLE 4.—Percent total number of male and female *Dichelopandalus leptocerus* collected at all depths and times of year in four areas in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Area 1	Area 2	Area 3	Area 4	Total
Total males	54.4	49.3	57.4	70.6	53.0
Females/Stage I	42.2	39.7	36.7	26.1	38.9
Females/Stage II	1.0	1.8	1.1	1.1	1.4
Total non-ovigerous females	43.2	41.5	37.8	27.2	40.3
Ovigerous females	2.4	9.2	4.8	2.2	6.6
Total females	45.6	50.7	42.6	29.4	47.0
Total no. individuals	1,047	3,626	2,419	92	7,184

TABLE 5.—Percent total number of male and female *Dichelopandalus leptocerus* collected in all areas and times of year by depth range in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Shallow (12-25 m)	Moderate (25-50 m)	Deep (50-85 m)	Total
Total males	54.4	47.7	60.3	53.3
Females/Stage I	41.5	40.4	32.4	37.6
Females/Stage II	1.1	2.0	0.9	1.4
Total non-ovigerous females	42.6	42.4	33.3	39.0
Ovigerous females	3.0	9.9	6.4	7.7
Total females	45.6	52.3	39.7	46.7
Total no. individuals	812	3,015	2,299	6,126

[4]Since no internal sexual characteristics (such as oocyte development) were examined in this study, the breeding season was defined as the period of time when ovigerous females were observed and sizes (ages) at maturity as the sizes (ages) when females produce eggs. No comparable information for males (i.e., mating times or sizes (ages) at maturity) was available. As used in this paper, the breeding season was, strictly speaking, the period of time between spawning and hatching when eggs were incubated.

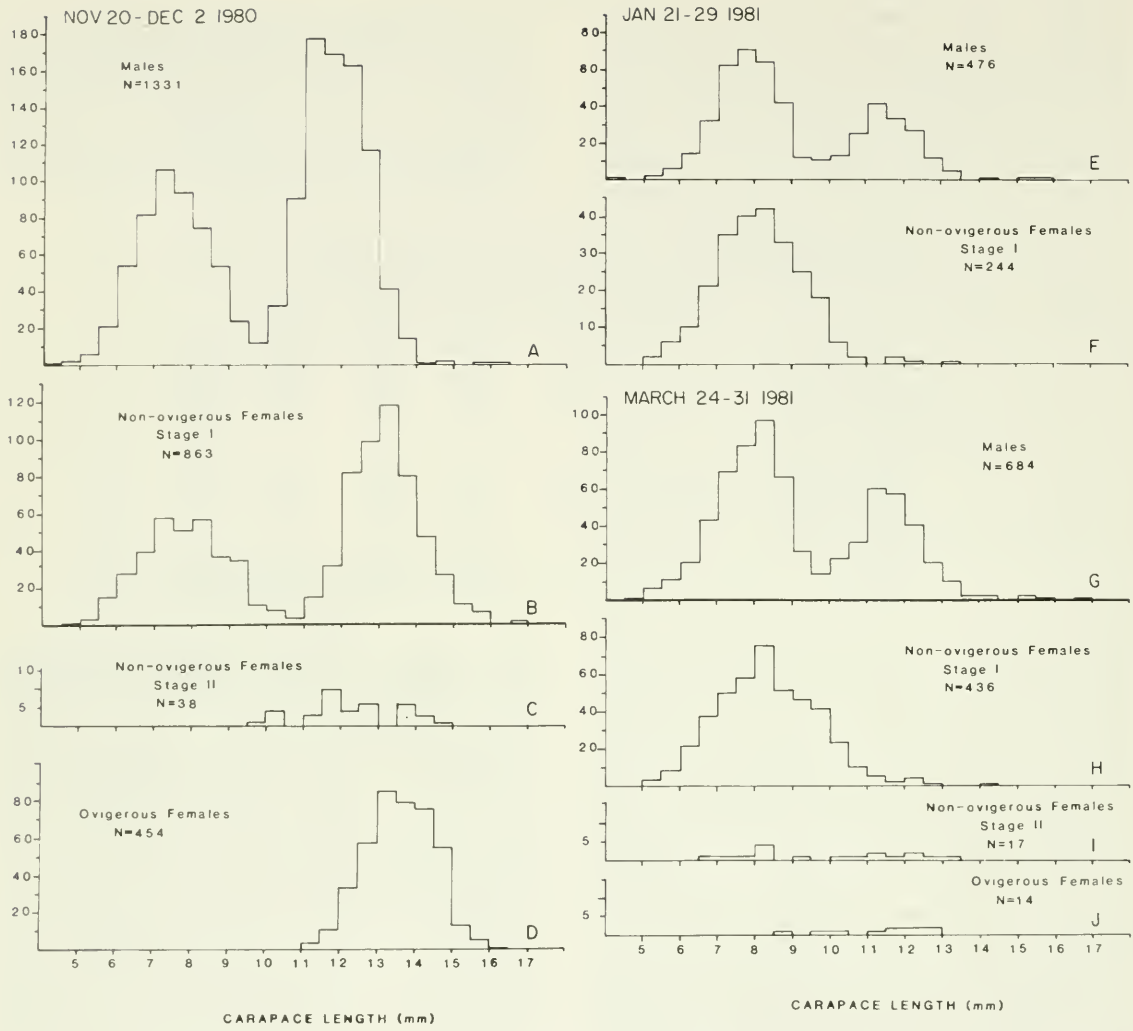
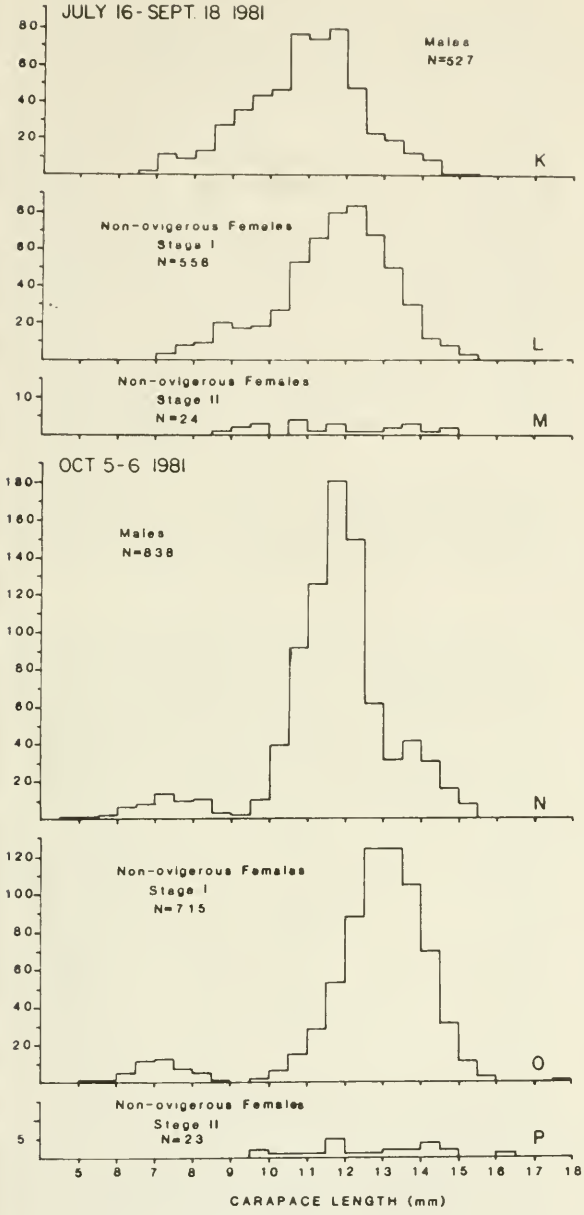


FIGURE 2.—*Dichelopandalus leptocerus* numerical length-frequency distributions by sex and reproductive stage.

TABLE 6.—Percent total number of male, transitional, and female *Pandalus montagui* collected at all locations and depths in Penobscot Bay during five sampling periods in 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	11/20-12/2 1980	1/21-1/29 1981	3/24-3/31 1981	7/16-9/18 1981	10/5-10/6 1981	Total
Total males	73.2	85.2	68.4	37.3	34.3	68.9
Transitionals	0.3	2.5	15.4	5.7	1.5	6.9
Females/Stage I	7.8	6.1	15.9	50.4	61.2	18.2
Females/Stage II	0.3	0.0	0.0	6.7	3.0	1.2
Total non-ovigerous females	8.1	6.1	15.9	57.0	64.2	19.4
Ovigerous females	18.4	6.2	0.4	0.0	0.0	4.8
Total females	26.5	12.3	16.2	57.0	64.2	24.2
Total no. individuals	332	871	800	405	67	2,475



were collected between November and April). A few females were still carrying eggs the following June. Hatching began in the winter and continued through June. *Pandalus montagui* populations studied in Penobscot Bay and Grand-Rivière spawned primarily in their second and third years. Females in the North Sea, on the other hand, were fully mature during their first year (Mistakidis 1957; Allen 1963), but there was no evidence that individual age-groups spawned more often there than at Grand-Rivière or in Penobscot Bay.

At least two age-groups of ovigerous *P. montagui* were apparent in the winter samples (Fig. 3C, G), whereas only a single age-group of ovigerous *D. leptocerus* was observed (Fig. 2D). Length-frequency data suggested that older female *P. montagui* (age 2+) spawned before younger females (age 1); 57% of the ovigerous females collected in November-December were > 15 mm CL (Fig. 3C), whereas only 30% remained in the same size group in late January (Fig. 3G). Sample sizes were much too small, however, to clearly indicate how many spawning age-groups were present or whether older females spawned earlier than younger ones. Earlier completion of spawning by older females was reported by Mistakidis (1957) in the Thames estuary. In Penobscot Bay, the relative abundance of ovigerous females was higher in moderate and deep waters and in areas 2, 3, and 4 (Tables 5, 6).

The capture of a single 10 mm CL ovigerous female *P. montagui* in January (Fig. 3G) indicates that a few females mature and reproduce during their first year. This shrimp could have started life as a female or could have changed sex in the first year and therefore never functioned sexually as a male. Mistakidis (1957) reported that some 0 age-group males in the Thames estuary changed sex and functioned as females during their first year. Some individuals in both the Thames estuary and Northumberland began life as females and matured in their first year (Mistakidis 1957; Allen 1963).

Sex Transition

Unlike most other Pandalid species, the Penobscot Bay population of *D. leptocerus* was not hermaphroditic. Not a single transitional individual was identified in the over 7,000 shrimp which were examined. Furthermore, males and females recruited to the > 5 mm CL population in October of their first year in nearly equal numbers (Fig. 2N, P). The ratio of males to females for the entire survey period was 53:47 (Table 3). *Pandalus montagui*, on the other hand, is a protandric (sequential) hermaphrodite. Nearly 7% of the 2,475 individuals examined exhibited external morphological characteristics typical of transitional *P. borealis* (Allen 1959). The sex ratio was 69% males to 7% transitionals to 24% females (Table 6). Although *P. montagui* is clearly protandric, some individuals in Penobscot Bay either begin life as females or assume external female characteristics by late November of their first year.[5] These

[5]Individuals of protandric pandalid shrimp species which begin life as females are referred to as primary females; those which change

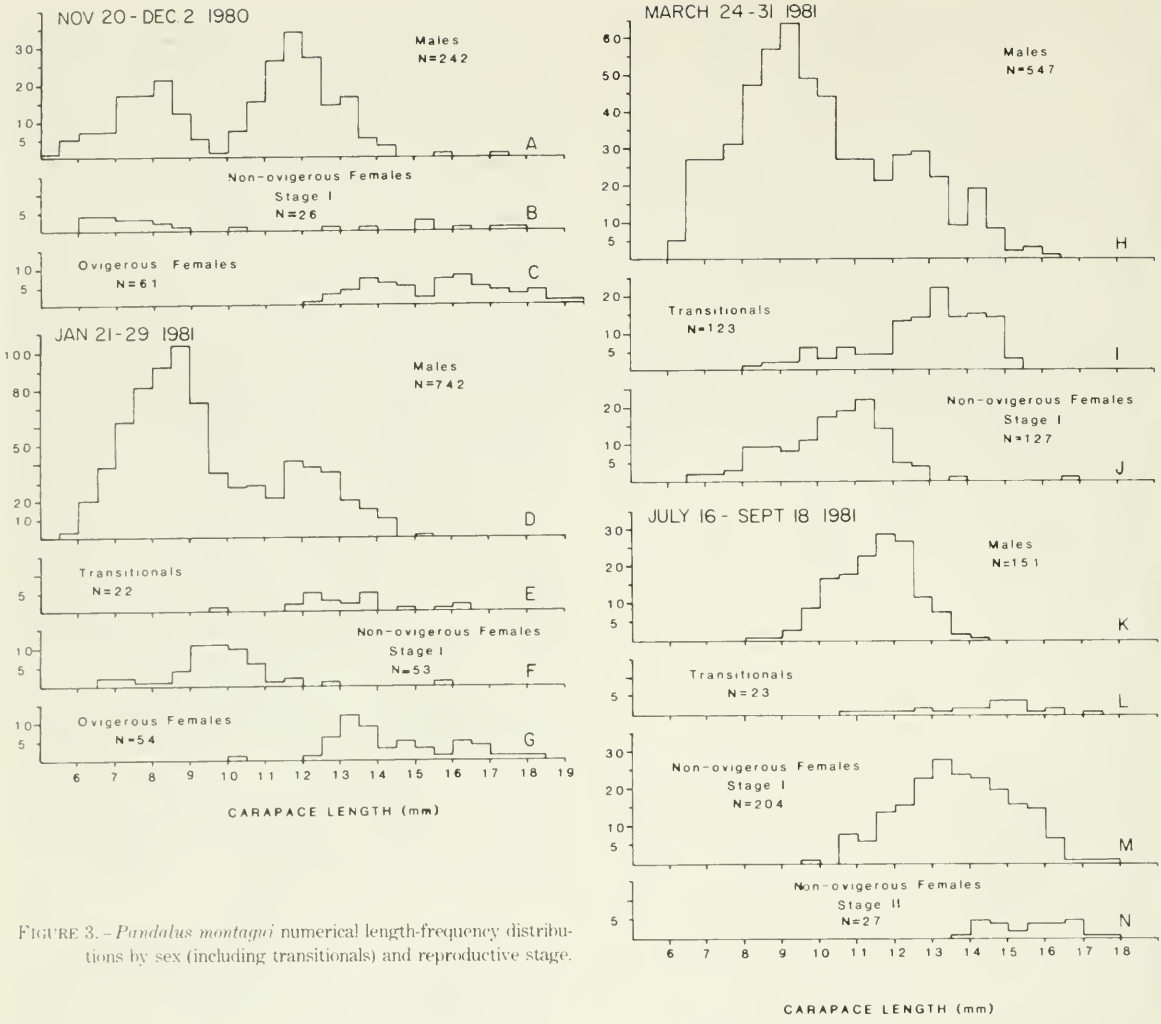


FIGURE 3.—*Pandalus montagui* numerical length-frequency distributions by sex (including transitionals) and reproductive stage.

females were obvious as a distinct size-group in the November-December length-frequency data at 6-9 mm CL (Fig. 3B). At this time, these females made up 15% of the newly recruiting 0 age-group. The relative abundance of 0 age-group females was considerably higher in the North Sea: 29-37% of most samples in the Thames (Mistakidis 1957) and about 50% in Northumberland (Allen 1963). On the other hand, only 11.2% of the age-1 *P. montagui* collected in May 1965 in Grand-Rivière were females (Couture and Trudel 1969b).

Size (Age) at Sex Transition

Transitional *P. montagui* were collected during all five sampling periods, but were most abundant in late March (Table 6) following the end of the breeding period. Sex transition apparently began in January, peaked in late March, and continued through the summer and early fall, reaching a minimum in late November. The rapid decline in the relative abundance of males after January 1981 and the accompanying increase in females after March (Table 6) indicated that shrimp, which functioned as males in the previous breeding season and became

sex in their first year following the repression of male sex characteristics and never function as males are called secondary females; and those which function first as males and then change sex are called hermaphroditic females (Mistakidis 1957). Since no distinction could be made in this study between the three types of female *P. montagui*, we have avoided the use of this terminology altogether and simply distinguish between individuals which remained as males during their first year, those which were females when they were first captured in November-December of their first year, and those which apparently changed sex during their first winter.

females prior to the subsequent breeding season, assumed external female characteristics during the winter and spring. The appearance of a distinct size-group of 9-11 mm CL females in late January (Fig. 3F) which was not present 2 mo earlier (Fig. 3B), suggests that transition was well underway by late January. The two size-groups of non-ovigerous females in January and March (Fig. 3I) were assumed to belong to the same age-group, the smaller females being those which did not function as males in their first year (they may have started life as females) and the larger females being those which were still males in November-December (Fig. 3A). Transitional shrimp made up a larger percentage of samples collected in moderate and deep waters and in areas 3 and 4 (Tables 7, 8).

Transition of the younger age-group which was first captured in November-December (Fig. 3A) was incomplete since a great many shrimp remained as males for another entire year before undergoing transition during their third spring (at age 2). Given the fact that a few male and transitional shrimp > 15 mm CL were sampled at various times of year, the possibility that a few individuals do not change sex until their fourth year (age 3) could not be ruled out. Even though the transition of younger (age 1) shrimp in the spring was incomplete, a sizable number of non-ovigerous Stage I shrimp which completed transition in their first year were collected in March (Fig. 3J). These new females were considerably larger (by about 2 mm CL) than their male counterparts, suggesting that it was the larger, faster growing, individuals which underwent transition at age 1. Allen (1963) also reported that the largest 0 age-group males changed sex first.

Older shrimp which changed sex in their second year had not yet appeared as females in March (Fig. 3J), suggesting that sex transition in older shrimp was delayed; it may also have been less rapid, particularly since growth was considerably reduced after the first year. Earlier studies of *P. montagui* indicated that sex transition in two locations in the North Sea persisted for most or all of the year. Mistakidis (1957) noted that sex transition occurred from May to December in the Thames estuary whereas Allen (1963) collected transitional individuals throughout the year in Northumberland, but primarily in June. The timing of minimal sex transition in Penobscot Bay and Northumberland was identical (November-December); Allen (1963) reported that this was when males were sexually active. Couture and Trudel (1969b) reported that most sex transition occurred in October at Grand-Rivière; a few transitionals were collected in July and August but none in May and June. Sex transition in the North Sea, as reported by Mistakidis (1957) and Allen (1963), was accelerated in comparison with Penobscot Bay; some individuals changed sex in their first year, but most did so in their second year. Ages at sex transition at Grand-Rivière, on the other hand, were the same as in Penobscot Bay, i.e., some in their second year, most in their third year, and some in their fourth year.

TABLE 7.—Percent total number of male, transitional, and female *Pandalus montagui* collected at all depths and times of year in four areas in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Area 1	Area 2	Area 3	Area 4	Total
Total males	82.3	63.4	67.1	77.9	68.1
Transitionals	1.6	3.0	11.5	12.3	7.1
Females/Stage I	14.0	25.4	16.8	5.5	18.8
Females/Stage II	0.0	2.6	0.4	0.0	1.3
Total non-ovigerous females	14.0	28.0	17.2	5.5	20.0
Ovigerous females	2.2	5.7	4.2	4.3	4.7
Total females	16.1	33.6	21.4	9.8	24.8
Total no. individuals	186	1,037	827	326	2,376

TABLE 8.—Percent total number of male, transitional, and female *Pandalus montagui* collected in all areas and times of year by depth range in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Shallow (12-25 m)	Moderate (25-50 m)	Deep (50-85 m)	Total
Total males	82.4	61.6	75.3	68.7
Transitionals	1.1	5.8	7.1	5.9
Females/Stage I	14.2	24.0	10.9	18.1
Females/Stage II	0.0	2.7	0.1	1.5
Total non-ovigerous females	14.2	26.6	11.1	19.6
Ovigerous females	2.3	5.9	6.6	5.8
Total females	16.5	32.6	17.6	25.4
Total no. individuals	176	1,013	732	1,921

Seasonal Changes in Size (Age) Composition

Two size-groups of male *D. leptocerus* were observed in the Penobscot Bay during the winter (Fig. 2A, E, G) and only one in the summer (Fig. 2K); similarly, female length-frequency distributions in November-December were bimodal (Fig. 2B), but a single size-group was dominant in the summer (Fig. 2L). Presumably, most of the older (age 2) males either die or migrate out of the upper Bay in the

spring since the younger age-group made up the entire population in the summer. Most of the females apparently spawn once and die after their eggs are hatched since very few older females were found in the winter. The presence of a few larger males in October (Fig. 2N) suggested that a few survive into their third fall and mate twice (or three times if they mature during their first year). Further evidence that most female mortality occurs following hatching while male mortality is delayed until later in the spring was indicated by the seasonal changes in relative abundance of males and females (Table 3): females decreased from 50 to 35% of the population between early December and late January while males decreased more slowly from 65% in January to 48% in the summer.

Age-2 *P. montagui* which were either in transition or were still males in March had mostly become females by the summer (although a few transitionals and large males still remained). The single large size-group of first-maturing Stage I females in the summer (Fig. 3M) presumably included age-1 females at a modal length of 13 mm CL and age-2 females at about 15 mm CL. At the same time, there appeared to be at least two size-groups of Stage II females in July-September (Fig. 3N) which had carried eggs the previous winter (Fig. 3C, G). Ovigerous females captured in November-December 1980 (Fig. 3C) presumably included first-time spawners at 12-15 mm CL and one or two groups of repeat spawners at 15-19 mm CL. Excluding the single female at 10 mm, two or three age-groups of ovigerous females were apparent in January (Fig. 3G). As indicated earlier, the relative abundance of the different age-groups in November-December and January showed that repeat spawners may have accounted for a larger percentage of the ovigerous females earlier in the winter.

Growth and Longevity

Male and female *D. leptocerus* which hatched in the winter of 1979-80 reached 6.0-8.5 mm CL by October of their first year (Fig. 2N, P) and grew relatively slowly during their first winter; by March they had reached 7-10 mm CL and the females were slightly larger than the males (Fig. 2G, H). This difference in size-at-age was also discernible in January (Fig. 2E, F). Growth was rapid during the spring of the second year prior to the beginning of the breeding season: males increased about 3 mm in carapace length by the summer while females increased by 4 mm (Fig. 2K, L). The difference in modal lengths between males and females had increased further by October (Fig. 2N, P) as growth increased modal carapace lengths by an additional 0.5-1.0 mm for both sexes. Growth between early October and late November when ovigerous females were first sampled was negligible, if October 1981 data can be compared with November 1980 data. During this same short period of time the relative abundance of the younger, newly recruited, age-group (males and females) increased dramatically. (A reduction in somatic growth can be expected at a time of rapid egg development since female growth ceases once their eggs have "dropped" and they are unable to molt). This species reached a maximum observed size of 19 mm CL (not included in compiled length frequencies), but most individuals did not exceed 16 mm CL. Unless older individuals migrate completely out of Penobscot Bay and were therefore not sampled during this survey, the maximum lifespan of *D. leptocerus* in the Bay appears to be about 2 yr and 9 mo, although the bulk of the population apparently survives for only 2 yr.

The first evidence of newly recruited 0 age-group *P. montagui* was in November-December 1980 (Fig. 3A, B). Individuals which remained as males during their second year grew from about 7-9 mm CL in November-December of their first year to 8-10 mm CL in March (Fig. 3H) and 10-13 mm CL in their second summer (Fig. 3K). As was observed for *D. leptocerus*, the growth rate increased in the spring. Age-1 shrimp which became females during their second spring reached 10-12 mm CL in March (Fig. 3J) and 12-15 mm CL in the summer (Fig. 3M). Comparison of November-December 1980 and January 1981 data (Fig. 3C, G) with summer 1981 data suggested that growth of mature females in the fall was negligible; the same was true for the males. The maximum observed size was 19.5 mm CL; females as large as 17-18 mm CL were collected in the winter (Fig. 3C, G). These results suggested that *P. montagui* in Penobscot Bay normally spend 1-2 yr as males and as many as 3 yr as females. The maximum lifespan is probably 4 yr since shrimp that remain males for 2 yr do not complete sex transition until their third year and function as females in their third and fourth years.

Growth at Grand-Rivière was sufficiently slower that males there were 2-3 mm CL smaller by the end of their first year than they were in Penobscot Bay. This difference in growth could be a result of lower summer bottom temperatures in the Gulf of St. Lawrence. A temperature range of – 1°C (in May) to 3°C (in October) was reported in 54 m at Grand-Rivière in 1965 (Couture and Trudel 1969a). Temperatures recorded in lower Penobscot Bay during the same months of the year at 40-60 m were

considerably higher, i.e., 3°C west of Islesboro in May 1970[6] and 11°-12°C at various stations in the lower Bay in August 1976[7]. In Penobscot Bay, *P. montagui* were smaller after their first year's growth than in the two North Sea locations (Mistakidis 1957; Allen 1963) but attained approximately the same size by the end of the second year. Males in the Thames estuary measured 10 mm average CL by November of their first year, and in Northumberland (at 40-60 m depth) they averaged 9.5 mm CL by October; transitionals reached 12.5 mm CL by November of their second year in both locations as compared with 11-13.5 mm CL males of the same age in Penobscot Bay (Fig. 3A), while females in Northumberland reached 14.8 mm CL by November of year 2 as compared with 13-15 mm CL at the same age in Penobscot Bay (Fig. 3C). One-year-old females in Northumberland averaged 10.8 mm CL in October.

Allen's (1963) explanation for this difference between male and female lengths-at-age was that shrimp which mature as females in their first year do so 3-4 wk after males of the same age-group; since growth virtually ceases in the fall and winter, the difference in length attained by the females in the first year is maintained into the third year of life. In Penobscot Bay, on the other hand, very few females mature in their first year; however, if males mature in their first year (this was not determined) and stop growing in the fall before the females, Allen's explanation might apply. It seems more likely that sex transition is a function of size, not age, and that the faster growing 0 age-group shrimp complete sex transition in their first year. Another possible explanation for the difference in size of females which change sex in their second and third years is that there may be two distinct periods of larval production and/or survival. Length-frequency data collected at two different periods during the winter (Fig. 3C, G) did suggest that older females may have spawned earlier than younger females. A 5-yr study of *P. borealis* in the Sheepscot River of Maine[8] failed, however, to reveal any consistent bimodality in larval production during February-April even though at least two age-groups of ovigerous females are commonly observed in commercial catch samples[9]. We contend, therefore, that the most plausible explanation for differences in the sizes of shrimp which become females in their second and third years is a difference in growth rates, especially since a similar difference in size was observed between male and female *D. leptocerus* in which sex remains fixed throughout life.

Pandalus montagui which either began life as females or became females early in their first year were smaller than their male counterparts by November-December of their first year (Fig. 3A, B). It therefore seems probable that the smaller Stage I (6.5-8.5 mm CL) females captured in late January (Fig. 3F) did not grow as rapidly as the larger females in the same age-group which apparently completed sex transition in late December and early January or as shrimp which remained as males for the entire year (Fig. 3D). These differences in length-at-age between 0 age-group males and both groups of females were also evident in late March (Fig. 3H, J). The accelerated growth rate of 0 age-group individuals which changed sex during their first year contrasts with the reported faster growth of *P. montagui* in the North Sea and at Grand-Rivière which began life as females (Allen 1963; Couture and Trudel 1969b).

Winter Migration

During November-December 1980, younger male and non-ovigerous female *D. leptocerus* were predominant in shallow water in area 1 (Figs. 4A, 5A) while the older age group predominated in deeper water (Figs. 4B, C, 5B, C). By late January, the older females were no longer being caught, and the older males had disappeared completely from depths < 50 m (Fig. 4D, E), but accounted for about 50% of the males collected in deep water in area 3 (Fig. 4F). There were older males in areas 2 and 3 (moderate and deep water) in March (Fig. 4G, H). These results suggested that older male shrimp migrated down the Bay into deeper water as the winter progressed and as bottom water temperatures dropped from about 8°C in early December to 1°C in late February and early March in the upper Bay.[10] Their disappearance from the catches,

[6]Muirhead, C. R., and J. H. Wartha. 1971. Temperature-salinity observations, Penobscot Bay, Maine, 1970. Oper. Data Rep. NOS DR-13, U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Off. Mar. Surv. Maps, Oceanogr. Div., Descr. Oceanogr. Sect., Rockville, MD.

[7]Central Maine Power Co., unpublished data, courtesy Richard Birge, Environmental Studies Department, CMP, August, ME.

[8]Stickney, A. P. Environmental physiology of northern shrimp, *Pandalus borealis*. Maine Dep. Mar. Resour., West Boothbay Harbor, ME, Annu. Rep. 1981-82, 15 p.

[9]Diodati, P., S. H. Clark, D. McInnes, R. Tichko, and D. Sampson. 1983. Gulf of Maine northern shrimp stock status -1983. Northern Shrimp Technical Committee, November 1983, 9 p.

[10]Birge, R. P. 1982. Surface and bottom water temperatures, upper Penobscot Bay, Maine, March 1975 - December 1981. Central Maine Power Co., Environmental Studies Department, Report SI-82-3, 45 p.

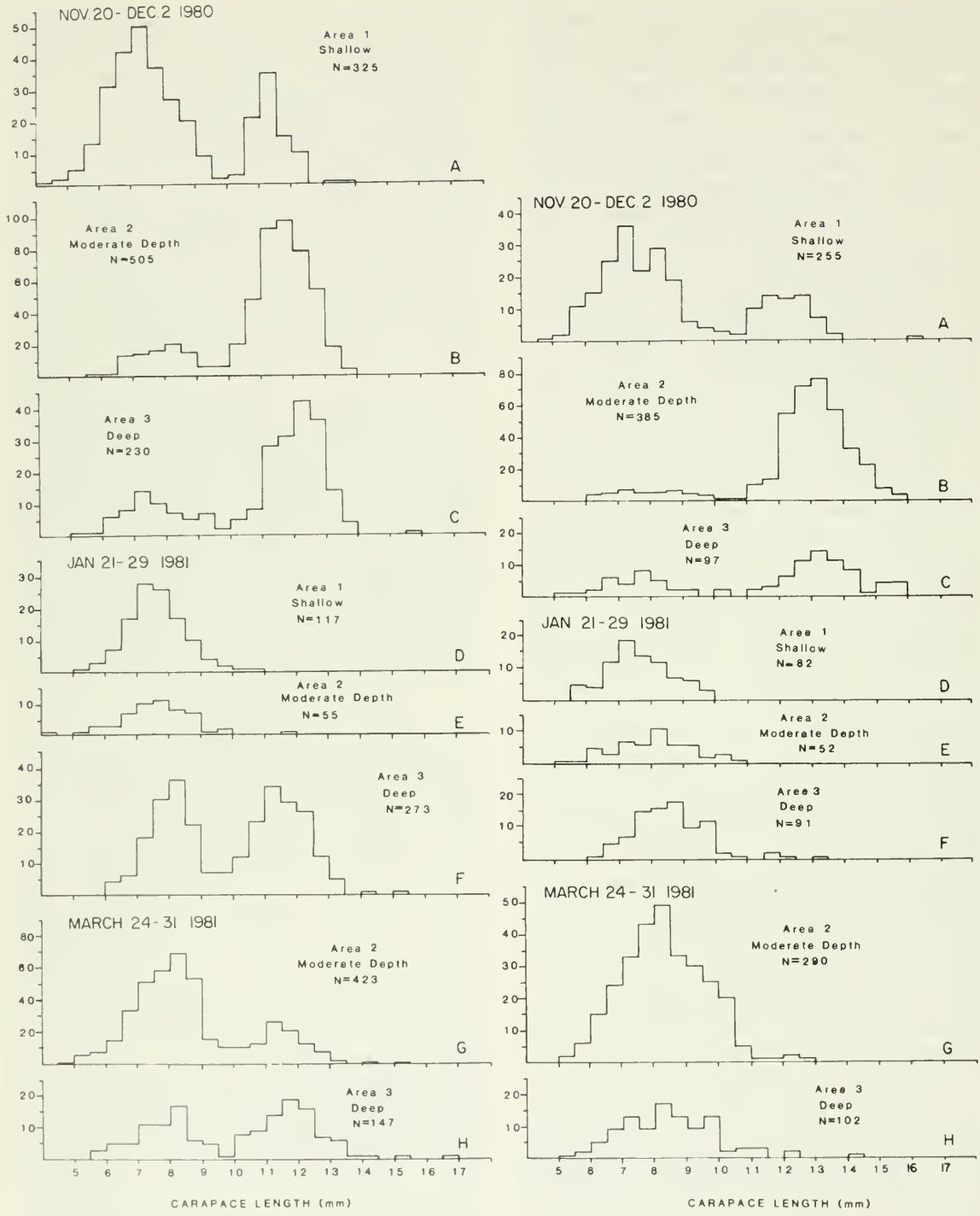


FIGURE 4.—Male *Dichelopandalus leptocerus* numerical length-frequency distributions by area and depth range.

however, may still have been a result of mortality rather than migration. The depth-area length-frequency data also revealed that slightly larger shrimp of both sexes and age-groups were captured in deeper water further down the Bay, suggesting that larger individuals are more likely to migrate than smaller ones.

Older male *P. montagui* also migrated down the Bay into deeper water during the winter: older age-1 males were more abundant than younger 0 age-group males in areas 2 and 3 (moderate and deep water, respectively) in November-December 1980 (Fig. 6A, B, C) and by late January nearly all the older males were in deep water in area 3 (Fig. 6D, E, F), but were not as abundant as the younger males in deep water in area 4 (Fig. 6G). There was no clear evidence that the larger males in either age-group were more frequent in deeper water and not enough females were collected during any single sampling period to permit an analysis of differential distribution of different age-groups by depth.

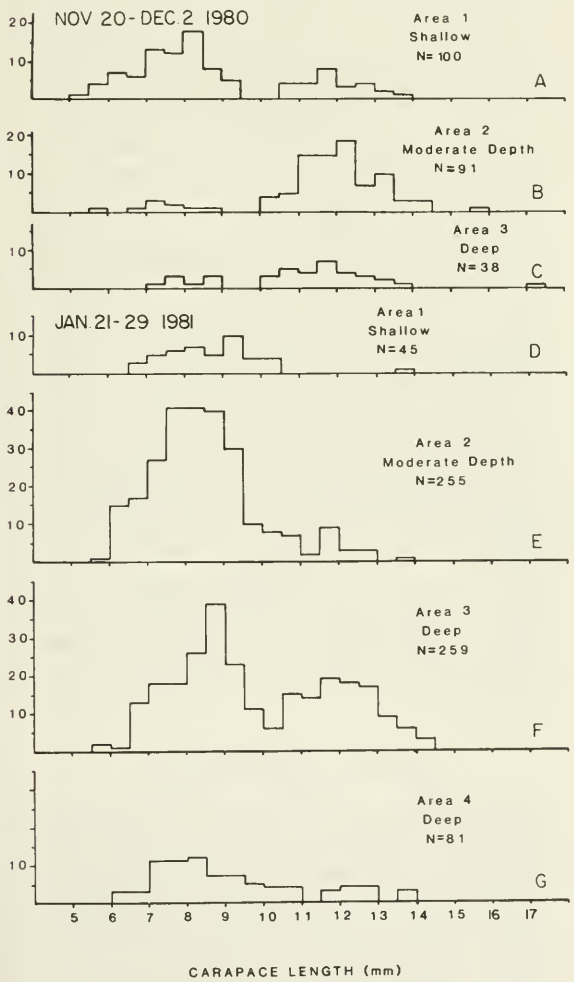


FIGURE 6.—Male *Pandalus montagui* numerical length-frequency distributions by area and depth range.

Allen (1963) reported an offshore migration of age-1 males to deeper water in the spring and summer in Northumberland waters; Couture and Trudel (1969a) observed the same phenomenon in Grand-Rivière in the summer as the temperature exceeded 6°C and reported that it was triggered by the onset of maturity; earlier maturing males migrated sooner than later maturing males, indicating that migration was a function of size, not age. Mistakidis (1957) and Allen (1963) both reported an offshore migration of *P. montagui* females in the fall; Allen, however, reported that the smaller females stay behind to spawn in shallow water and that there was no "massive" return migration in the spring whereas Mistakidis reported a general offshore fall migration of females and a return migration in the spring. Allen (1963) reported that females in Northumberland which survived to spawn a third time were only found in depths > 100 m.

CONCLUSIONS

This study of the life histories of *Pandalus montagui* and *Dichelopandalus leptocerus* in Penobscot Bay has revealed some notable differences in reproductive characteristics and (apparently) in longevity between the two species. On the other hand, growth rates and migratory behavior were similar.

Most importantly, *P. montagui* is hermaphroditic; *D. leptocerus* is not. In 1980-81, some transitional *P. montagui* were observed during all five sampling periods, but were most common in the early spring; most individuals change sex at the end of their second year but some do so during their first year and a few may not change sex until their third year. Some individuals apparently begin life as females; 15% of the 0 age-group which recruited to trawl catches at 5-10 mm CL in November-December 1980 were females. Ovigerous *P. montagui* were collected over a longer time period, owing, at least in part, to the presence of more age-groups in the spawning population. Most *D. leptocerus* females spawn during their second year, although a few also spawn in their first year; ovigerous females were collected primarily in late November-early December. *Pandalus montagui* spend 1-2 yr as males; individuals which undergo sex transition in their second year may function as females during their second, third, and fourth years while those which change sex in their third year may only function as females for 2 yr. Judging from the

length-frequency data collected during this study, it is unlikely that very many *P. montagui* survive in the Bay beyond age 4. No *D. leptocerus* females older than age 2 were caught in the Bay although some males remained until their third fall (age, 2 yr and 9 mo). Conclusions concerning longevity were complicated by the fact that larger individuals of both species migrated down the Bay into deeper water as the winter progressed and were not captured and by the difficulty of inferring age from length data for the larger size-groups, particularly for *P. montagui*.

Both species were similar with respect to growth and migratory behavior. Growth decreased with increasing age and was seasonal, i.e., rapid in the spring and summer of the first year and the spring of the second year and negligible in the fall and winter. Males of both species reached 7-9 mm CL at age 1 and 11-13 mm CL at age 2. The data suggested that early (age 1) transitional *P. montagui* also grow considerably more rapidly than the remainder of their age group which undergo sex transition at age 2. The slowest observed growth rate was for *P. montagui* which apparently begin life as females and therefore never undergo sex transition. For *D. leptocerus*, females grow more rapidly than males and differential growth is a "fixed" sexual attribute. For *P. montagui*, the fact that the faster growing individuals change sex a year earlier and therefore function as females for an additional year (assuming that fast- and slow-growing shrimp have identical lifespans) means that more rapid growth and early sex transition increase the reproductive potential of the population, as long as enough males remain in the population to mate with the females. Female maturity is clearly a function of size, not age.

The life cycle of *P. montagui* in Penobscot Bay was quite different in several respects from the life cycles of populations which have been studied in the North Sea and at Grand-Rivière, Quebec. *Pandalus montagui* populations in two locations in the North Sea (Mistakidis 1957; Allen 1963) appeared to grow more rapidly in their first year of life than in Penobscot Bay and were composed of a considerably greater proportion of early maturing females, many of which never functioned as males. Growth over the entire lifespan was considerably more rapid in Penobscot Bay and the North Sea than at Grand-Rivière (Couture and Trudel 1969b), but the relative scarcity of females which do not function first as males and the delay of most sex transition until the third year were common to the Canadian and United States populations. In addition to a difference in the timing of maximum sex transition from age 2 (Penobscot Bay and Grand-Rivière) to age 1 (North Sea), the seasonal intensity of sex transition was not the same in three of the populations. Most transitionals were observed in March in Penobscot Bay, in June in Northumberland (Allen 1963), and in October at Grand-Rivière (Couture and Trudel 1969b). Eggs were carried by females in both North Sea locations and in Penobscot Bay during the winter (November-March); at Grand-Rivière most ovigerous females were observed in October.

In Penobscot Bay and the North Sea, sex transition tended to follow the end of the breeding season, whereas in Grand-Rivière, maximum sex transition coincided with the time when most females were carrying eggs (unless sex transition was more common later in the fall when no samples were collected), suggesting that there was a 12-mo interval between the appearance of external female characteristics and spawning at Grand-Rivière, and a 6-9 mo interval in Penobscot Bay and Northumberland. More rapid growth rates in the latter two locations would explain the shorter time intervals between sex transition and spawning. The reproductive cycle in Grand-Rivière was seemingly continuous, beginning in July and ending in June (Couture and Trudel 1969b).

Although an offshore migration of larger male *P. montagui* was observed in Penobscot Bay, Grand-Rivière, and Northumberland, this migration occurred in the winter following the end of the spawning season in the Bay and in spring and summer, prior to spawning, in the other two locations. Similar movements of larger females have been noted in both North Sea populations in the fall. Unlike the other migrations, the one observed in Penobscot Bay was not a spawning migration and may instead have been a response of older shrimp to declining winter temperatures in the shallower waters of the upper Bay. The departure of significant numbers of older shrimp from the Bay could certainly affect any conclusions concerning the size or age structure of either population and their estimated maximum lifespans.

ACKNOWLEDGMENTS

The authors wish to acknowledge Frank Spencer, Director of the Fisheries Technology Division, and Penn Estabrook, Director of the Bureau of Marine Development, both of the Maine Department of Marine Resources (DMR), whose support made this project possible. Thanks are also due to Mike Brown, formerly a DMR employee and leader of this project; to Mike Dunton, the captain of the RV *Explorer* and to the late Paul DeRocher, captain of the RV

Challenge; to Curt Crosby for assisting with the field work; to Margaret Hunter, who supervised the computer analysis of the data; to Pat Hoyt and Vicki Averill, who typed many copies of the manuscript; to Patti Millette and Kim Knowlton who drafted and photographed the figures; to Richard Birge of Central Maine Power Company who kindly supplied us with temperature data for Penobscot Bay; and to Steve Clark of the Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, for his constructive review comments.

This research was supported by NOAA Grant NA-81AA-D-00035 to the University of Maine and the University of New Hampshire Sea Grant College Program and by the Fisheries Technology Division of the Maine Department of Marine Resources.

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VISUAL THRESHOLD FOR SCHOOLING IN NORTHERN ANCHOVY *ENGRAULIS MORDAX*

JOHN HUNTER AND RAGAN NICHOLL[1]

ABSTRACT

The visual threshold for schooling was determined for two groups of 50 adult northern anchovy in the laboratory. The index of dispersion and the mean distance to the nearest neighbor were used to measure changes in schooling as a function of light intensity. The threshold light intensity for schooling, 6×10^{-11} W cm^{-2} (2.6×10^{-4} mc), was estimated to occur at a depth of 30 m on a starlit night and at 38 m during a full moon, when the chlorophyll concentration is 0.2 mg Chl a m^{-3}. At 2.0 mg Chl a m^{-3} the threshold occurs at a depth of 8 m on a starlit night and at 20 m under full moon light. Sufficient light appears to exist at night within the upper 10 m for schooling to occur in most of the habitat of the anchovy. The vertical distribution of newly spawned anchovy eggs indicated that the maximum depth of spawning may be similar to the maximum depth of schooling and that the visual threshold for schooling could be used to forecast maximum spawning depth in the sea.

Vision plays a primary role in the maintenance of most fish schools in the sea. Other sense organs, particularly the lateral line, are important in coordinating movements and spacing of fish within the school (Pitcher et al. 1976), but it is unlikely that lateral line sense alone is sufficient for maintaining the integrity of schools at night in the sea. In fact, a large number of laboratory studies indicate that if light is sufficiently reduced, fish no longer maintain schools (Whitney 1969; Blaxter 1970). Thus the visual threshold for schooling and the depth of penetration of light probably determine the maximum depth at which pelagic fishes are able to school at night in the sea.

Our objective was to determine the visual threshold for schooling in adult northern anchovy, *Engraulis mordax*, and to use this information to forecast the maximum schooling depth for anchovy at night in the sea. This calculation is of ecological interest because the maximum depth for schooling is probably also the maximum depth for spawning and for nocturnal feeding. Anchovy spawn only at night and visual recognition of other fish is probably as essential for spawning as it is for schooling. During what we believe was spawning behavior, several males rapidly pursued a female over an irregular path, a tactic probably not possible using senses other than vision. This is a casual laboratory observation and requires further documentation, however.

Northern anchovy feed at night as well as in the day (Loukashkin 1970; Hunter and Kimbrell 1980). Light may not be necessary for filter feeding, but it is essential for particulate feeding, although somewhat higher light levels may be required for feeding than for schooling (Hunter 1968). Anchovy migrate toward the surface at sunset (Mais 1974), and schools are less frequently detected at night using sonar and not detected with echo sounders (Smith 1970). Nevertheless, no doubt exists that schooling continues at night because the anchovy fishery is typically a night fishery and because profiles of schools are detectable at night owing to the bioluminescent disturbances their movements produce (Squire 1978).

METHODS

Apparatus and Laboratory Procedures

Two groups of 50 northern anchovy (group 1, mean length = 10.5 cm SL; group 2, = 9.8 cm SL) were maintained in a 4.6 m diameter tank supplied with running seawater (group 1, mean temperature = 16.9°C; group 2, 21.0°C). To simplify photographic analysis the school of 50 fish was constrained to a somewhat two dimensional form by maintaining them in water 45 cm deep. The fish were fed adult *Artemia* at the daily time of 1000, and the tank was cleaned 1 h after feeding.

The tank, which was constructed of blue vinyl, was located in a light tight rectangular enclosure in which the walls and ceiling were covered with white vinyl

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted August 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

to diffuse the light. Four light sources were equally spaced around the periphery of the tank; the top of each being just below the tank rim. Each source consisted of a 30 W tungsten microscope lamp with reflector enclosed in a tube. On top of the tube were two color filters; a green acrylic plastic filter (#2414, Rohm and Haas), and a sealed petri dish containing a 5% $CuSO_4$ solution (by weight). To diffuse the light a translucent white acrylic filter (#W-2447, Rohm and Haas) was placed on top of the color filters and light transmitted by the white filter entered a white opal glass globe (13 cm diameter) that formed the top of the source. The lamps were operated for 5 h (10% of lamp life) before they were used to produce test levels of irradiance. These sources were used to produce four test levels of irradiance during a 12-h night. Additionally, four tungsten 100 W household lamps (unfiltered) with reflectors were used for the daytime level of irradiance. These lamps were placed at regular intervals around the perimeter of the tank near the ceiling. Light from these lamps reflected off the ceiling providing a uniformly diffuse illumination. The spectrum produced by the four sources (Table 1) resembles the greenish spectrum typical of anchovy habitat, but the spectrum used in the day was not different from a standard curve for a tungsten lamp and consequently contained an unnaturally high proportion of longer wavelength energy. Our term for the condition when all lamps were off was darkness; under these conditions light was not detectable by a dark adapted human observer and the irradiance was below the sensitivity of a 931A photomultiplier which can detect about 5×10^{-6} mc (meter candle).

To record the effect of light on the schools the fish were photographed from above the tank using a 35 mm automatic camera and flash attachment. The camera was controlled by a timer, and photographs were taken at 30-min intervals for 5 h during the 12-h day, at night in darkness, and at night at the test levels produced by the four sources. Night photographs were taken during a 5-h period commencing 2 h after the end of the 12-h day. Ten photographs were usually analyzed at each light level for each group, but in several tests, 1 or 2 photographs were not analyzed because not all 50 fish could be seen.

Two indices of schooling were calculated for each photograph: an index of dispersion (Pielou 1969), and the mean distance to the nearest neighbor (Hunter 1966). The dispersion index was calculated by superimposing a grid containing 326 quadrats over the projected image of the tank and counting the number of fish occurring in each quadrat. The variance mean ratio ($s^2/\bar{x}$) for the number of fish per quadrat was the index of dispersion. The index was calculated for each photograph, and an average index was computed for each light treatment (n = 8-10 photographs). A dispersion index of 1 indicates a random distribution, whereas higher values indicate aggregation (Pielou 1969) and imply the existence of schooling. Values < 1 imply a uniform distribution over the grid. The mean distance to the nearest neighbor was computed for a random subsample of 10 fish in a photograph. All 50 fish in a photograph were numbered and the subsample of 10 was selected by drawing the fish numbers from a table of random numbers. For each of the 10 fish in the subsample the distance in centimeters to its nearest neighbor was measured (distance between heads), a mean distance calculated for each photograph, and means

TABLE 1.—Spectral functions used to estimate the depth of occurrence of the visual threshold for schooling under the various water types and incident irradiances including spectral irradiance in the laboratory apparatus, moonlight at 3 m below water surface, starlight at the earth's surface (Munz and McFarland 1977), and the relative sensitivity of the dark adapted anchovy eye (*Engraulis encrasicholus*, Protasov 1964).

Wavelengths (nm)		Energy per 25 nm interval ($W\ cm^{-12}$)			Relative sensitivity anchovy eye
Mean	Interval luminaires	Laboratory luminaires	Moonlight at 3 m depth	Starlight at surface	
400	400-412	3.411×10^{12}			
425	413-437	1.346×10^{11}	6.109×10^{-10}	1.978×10^{-11}	0.16
450	438-462	3.402×10^{11}	6.689×10^{10}	2.418×10^{11}	0.53
475	463-487	6.822×10^{11}	6.820×10^{-10}	2.291×10^{-11}	0.85
500	488-512	9.631×10^{11}	7.072×10^{-10}	2.374×10^{-11}	1.00
525	513-537	1.069×10^{10}	7.067×10^{10}	2.449×10^{11}	0.75
550	538-562	9.618×10^{11}	7.283×10^{10}	5.125×10^{-11}	0.42
575	563-587	5.297×10^{11}	6.881×10^{-10}	2.838×10^{-11}	0.22
600	588-612	[1]9.494×10^{12}	5.481×10^{10}	3.874×10^{-11}	0.08

[1]Wavelength interval = 588-600 nm.

for each light treatment. These measurements are indices of only one characteristic of a fish school, the tendency of individuals to maintain contact with each other and thereby remain in a social group. The polarization of individuals in a school is frequently included in definitions of schooling as the cohesive movements of a school require that fish maintain relatively constant headings and individual distances which gives the polarized appearance of moving schools. This characteristic of fish schools was not measured in our study, thus the visual threshold we estimated was one for the maintenance of schooling in the broadest sense, that is the existence of a group maintained by visual attraction.

Radiometric Procedures, Calibrations, and Computations

Radiometric equipment used in this study consisted of an Optronics spectroradiometer (model 714-V) (calibrated against a radiometric standard) and a photometer (Gamma Model 700). The spectroradiometer was used to measure the spectral irradiance produced by the sources at full lamp output but the treatment levels of irradiance were below the sensitivity of the spectroradiometer. Absolute measurements of light intensity were made 25 cm above the water surface (the difference between this position and within the water would be < 10%). The light treatments were varied by placing neutral density filters in each of the light sources; the neutral density filters were calibrated on an optical bench. Test levels we used were computed from the filter factors for the neutral density filters. The photometer was used to check irradiance levels prior to a test, but we believe the computed values to be more accurate. Irradiance distribution in the tank was mapped using the photometer and the treatment values weighted by tank area so that they represented the average irradiance 25 cm above water surface.

Our laboratory estimates of the visual threshold for schooling were used to calculate the maximum possible depth of schooling in the sea for various levels of incident irradiation and water types. Threshold values in W cm^{-2} were converted to anchovy effective units (W $cm^{-2}_{anch.\ eff.}$) by weighting the spectrum in the apparatus by the relative sensitivity of the scotopic curve of the anchovy *Engraulis encrasicholus* from an electroretinogram by Protasov (1964) (Table 1). Two levels of night illumination were used, full moon at 3 m depth (2.78×10^{-9} W cm^{-2}), and starlight at the earth's surface (1.08×10^{-10} W cm^{-2}) (both measurements from Munz and McFarland 1977). The depth (meters) in the sea (Z) at which a given threshold (E_z) value occurred was calculated using the equation of Baker and Smith (1982):

$$Z = \frac{\ln \left(\frac{E_z}{E_0} \right)}{-K_t}$$

where E_0 is the incident radiation (full moon or starlight) in anchovy effective units. K_t is the wave length specific attenuation coefficient and is the sum of coefficients for pure water (K_w), dissolved organic matter (K_d), and chlorophyll a (K_c). Tables of coefficients, and equations for calculating these attenuation coefficients, are given by Baker and Smith (1982). In our calculations we assumed that the dissolved organic matter was constant at 0.7 mg l^{-1} which is typical of the anchovy habitat. We calculated K_c for a range of chlorophyll (Chl) a concentrations ranging from 0.1 to 10 mg Chl a m^{-3} and at 25 nm intervals from 425 to 600 nm for each Chl a concentration. Each K_t value for 25 nm increments was weighted by the appropriate anchovy scotopic sensitivity, and the average anchovy weighted $K_{t\ anch.\ eff.}$ was used in the final calculation of Z.

Many uncertainties and possible biases exist in such an extrapolation from laboratory to sea conditions: Cloud cover was not considered nor were possible effects of bioluminescence; spectral irradiance values for full moon and starlight of Munz and McFarland (1977) may not be representative of conditions in the anchovy habitat although they are relatively close to those given in photometric units by Brown (1952); variation in dissolved organic matter is not considered; the radiance distribution over 360° in the tank probably does not resemble that in the sea (only downwelling irradiance was considered here); use of the action spectrum based on an electroretinogram of a dark adapted *E. encrasicholus* eye instead of one for schooling of *E. mordax*; and of course, the usual statistical uncertainties. Despite these uncertainties and biases we believe our estimates of schooling depth are the most accurate to date thanks to the models developed by Baker and Smith (1982).

RESULTS AND DISCUSSION

The schooling threshold based on the index of dispersion was between 4.8×10^{-12} and 7.8×10^{-10} W cm^{-2} (Fig. 1; Table 2). At the lower value and in darkness the index of dispersion ($s^2/\bar{x}$ fish per

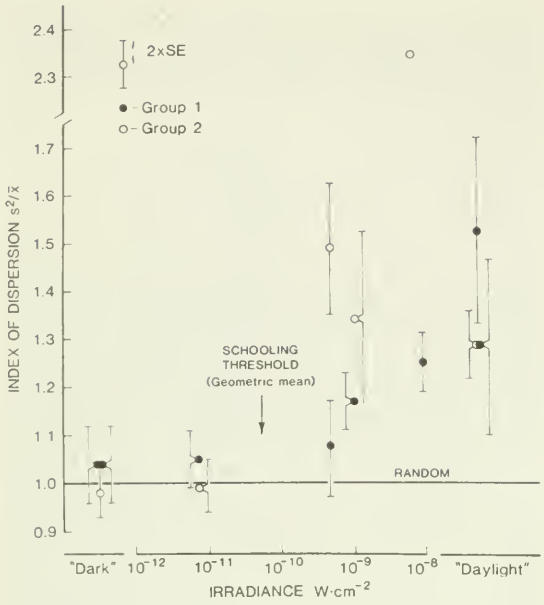

FIGURE 1.—Visual threshold for schooling in northern anchovy. Schooling is indicated by the index of dispersion ($s^2/\bar{x}$). A ratio of 1 implies no schooling as it indicates a random distribution. Each point is a mean calculated from 8-10 photographs and bars are ± 2 × standard error of the mean. No error bars are given for one value (2.34 ± 0.47) because it falls far beyond the rest of the values. Mean dispersion is shown for four test levels of downwelling irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" (1.496×10^{-5} W cm^{-2}) which was the normal daytime level of irradiance in the apparatus.

quadrat) did not differ from unity indicating that the fish were randomly distributed. Hence no schooling existed at the lower irradiance value and in darkness, whereas at the higher value the fish were clearly aggregated. These values delimit a region of about 2 log units of irradiance where one cannot be certain if schooling occurs or not. The actual threshold for schooling must fall somewhere in that region, and we have arbitrarily considered the threshold value to be the geometric mean irradiance of the above two irradiances (6×10^{-11} W cm^{-2}) thereby reducing the uncertainty in the threshold value to about 1 log unit. In subsequent tables and figures we give the upper and lower bounds of the region as well as the threshold value, however.

The variance of the dispersion index, a measure of the variation in school dispersion among photographs, increased sharply at irradiances above the threshold indicating a wide variation in the dispersion of fish among photographs. This can be expected because schooling fish react to fright stimuli, feeding, and many other conditions by altering interfish distances, thereby changing the cohesion or degree of dispersion of the school (Blaxter and Hunter 1982). At light levels below the visual threshold, fish are unable to respond socially to such stimuli, hence the variation among photographs is low.

Mean distance to the nearest neighbor followed the same pattern as we have described for the index of dispersion. Values in darkness and at the lower

TABLE 2.—Mean and standard deviation of the index of dispersion and mean distance to the nearest neighbor for various irradiance levels.

Irradiance (W cm^{-2})	Group	Schooling indices: Dispersion index ($s^2/\bar{x}$) $\bar{x}$	Dispersion index ($s^2/\bar{x}$) s	Mean distance to nearest neighbor (cm) $\bar{x}$	Mean distance to nearest neighbor (cm) s	Number of photographs
1.496×10^{-5} ("daylight")[1]	1	1.28	0.29	17.50	3.71	10
	1	1.52	0.30	12.15	4.10	10
	2	1.28	0.11	24.61	4.94	10
[2]8.92×10^{-9}	1	1.25	0.10	12.19	2.52	10
	2	2.34	0.74	19.49	5.50	10
[2]1.079×10^{-9}	1	1.17	0.09	16.65	3.86	10
	2	1.34	0.27	21.72	7.14	10
[2]4.777×10^{-10}	1	1.07	0.15	18.48	3.86	9
	2	1.49	0.21	18.05	6.62	10
[2]7.785×10^{-12}	1	1.05	0.09	21.87	5.39	8
	2	0.99	0.07	30.40	5.14	10
Dark[3]	1	1.04	0.12	21.20	4.16	9
	1	1.04	0.12	19.61	4.83	9
	2	0.98	0.07	34.12	6.36	10

[1]Unfiltered tungsten lamp.
[2]Filtered lamp - spectrum given in Table 1.
[3]Below sensitivity of 931A photomultiplier.

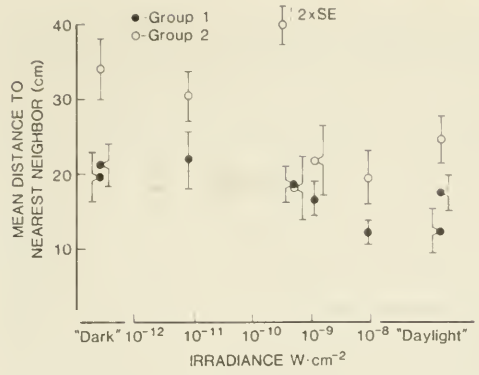

FIGURE 2.—Visual threshold for schooling in northern anchovy is indicated by changes in the mean distance to nearest neighbor. Each point is a mean calculated from 8-10 photographs and bars are ± 2 × standard error of the mean. Mean distance to the nearest neighbor is shown for four test levels of irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" (1.5×10^{-5} W cm^{-2}) which was the normal daytime level of irradiance in the apparatus.

irradiance values were not statistically different. Above the threshold the mean distance to nearest neighbor was lower than that in darkness indicating closer spacing among pairs, but no trend with light intensity seemed to exist above the threshold range (Fig. 2). For the purpose of estimating a threshold, however, we believe the index of dispersion is preferable because the criterion for randomness is well defined and the dispersion index takes into account all 50 fish, whereas we used only 10 random pairs per photograph for the nearest neighbor measurements which reduced its precision.

Our calculations indicate that in water of low chlorophyll concentration (0.2 mg Chl a m^{-3}) the threshold irradiance for schooling occurs at a depth of 38 m during a full moon and at a depth of 30 m on a starlit night (Fig. 3). The method of calculation is described in the Methods section on radiometric procedures. Light attenuates rapidly as Chl a concentration increases up to about 2 mg m^{-3} total chlorophyll; at 2.0 mg Chl a m^{-3} the schooling threshold occurs at a depth of only 8 m on a starlit night and at 20 m under full moonlight. Above 2 mg Chl a m^{-3} light attenuates more slowly with increasing Chl a concentration with the threshold at 10 mg Chl a m^{-3} falling at 5 m in starlight and at 12 m in full moonlight. These calculations indicate that sufficient light exists at night for northern anchovy to school within the upper 10 m of nearly all habitats under clear skies, but the maximum possible depth of the schooling would be expected to vary greatly with water type and incident light intensity. An order of magnitude decline in incident irradiation can be expected under the darkest storm clouds (Brown 1952); under these conditions schooling may not be possible at the highest chlorophyll concentrations.

It seems appropriate to use these visual thresholds as estimates of the maximum depth of spawning because spawning probably also depends upon the ability of anchovy to see one another. We calculated the vertical distribution of newly spawned anchovy eggs (0-4 h old, type "S") using data from the unpublished vertical distribution study of Pommeranz and Moser (1983). We selected sets of vertical samples at two stations for which surface Chl a concentrations had been measured and then calculated a mean Chl a concentration for an inshore and offshore series of net hauls. We then estimated the maximum depth for schooling assuming that the surface Chl a was equivalent to an integrated value for the water column as required by the Baker and Smith 1982 model. Spawning occurred closer to the surface at the inshore station which had a high Chl a concentra-

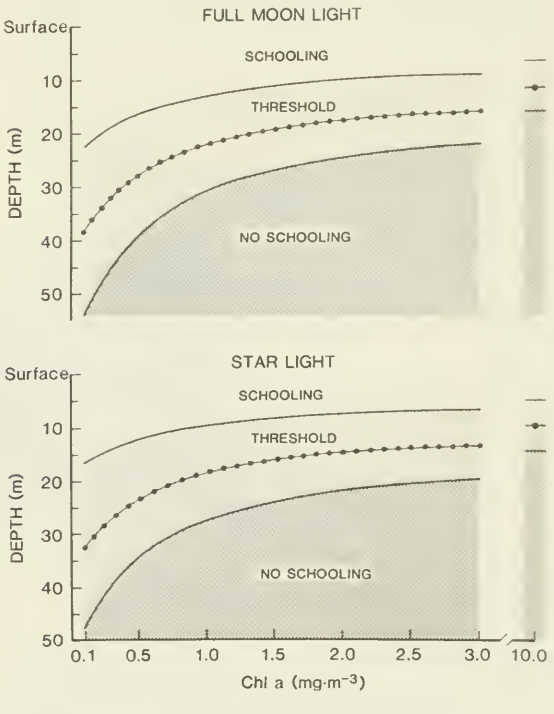

FIGURE 3.—Maximum depth of schooling of northern anchovy in waters of various chlorophyll concentrations (Chl a) under starlight and full moon. Coefficients used in calculations are in Table 1 and in Methods section. Darkly shaded area indicates proportion of water column where no schooling is expected, lightly shaded area indicates depth range of schooling threshold. Central dotted line is the geometric mean.

tion (1.5 mg m^{-3}) than at the offshore station which had a lower concentration (0.24 mg Chl a m^{-3}). At the onshore station only 4% of the eggs occurred below 20 m, whereas at the offshore station 31% were below 20 m. This difference is particularly striking because the inshore samples were taken under a full moon, whereas the moon was in the first quarter when the offshore station was occupied. At both stations the predicted maximum depth for schooling was close to the observed maximum depth for newly spawned eggs (Fig. 4). We may have underestimated the depth of schooling for the offshore (low Chl a) station as we used a starlight value of Munz and McFarland (1977) because no data existed for 1/4 moon. Spawning occurred prior to moonset since spawning occurs between the time of 1800 and 2400 and moonset varied from about the time of 2130 to 0200 (19-25 March 1980). In addition, the offshore station had a deeper mixed layer (about 35 m) than the inshore station (about 10 m) and vertical distribution of anchovy eggs and larvae also may be affected by the depth of the mixed layer (Ahlstrom 1959). Regardless of these uncertainties, these data indicate that underwater visibility may set the maximum depth for spawning of anchovy, although other factors, such as low temperature, might constitute an additional barrier to spawning schools. Thus fish visual thresholds may be a convenient way to establish a general function for estimating the maximum depth of spawning for anchovy and perhaps other pelagic spawning clupeoids in all habitats. Such a general function, that could account for much of the variation in the maximum depth of eggs, could be quite useful in three dimensional models of larval transport or predation. A spawning-depth, water-type function based on visual thresholds seems particularly attractive owing to the considerable cost of accurately measuring the vertical distribution of eggs and larvae even in a single habitat let alone the cost for estimating it for all possible spawning habitats of the population.

To compare the northern anchovy schooling threshold to literature values we converted our radiometric measurements to lux or meter candles (mc), by weighting the spectral irradiance in the apparatus by the human photopic curve, as the literature values are largely in photometric units (see reviews by Whitney 1969 and Blaxter 1970). The visual threshold for anchovy schooling (2.6×10^{-4} mc, Table 3) is about an order of magnitude higher

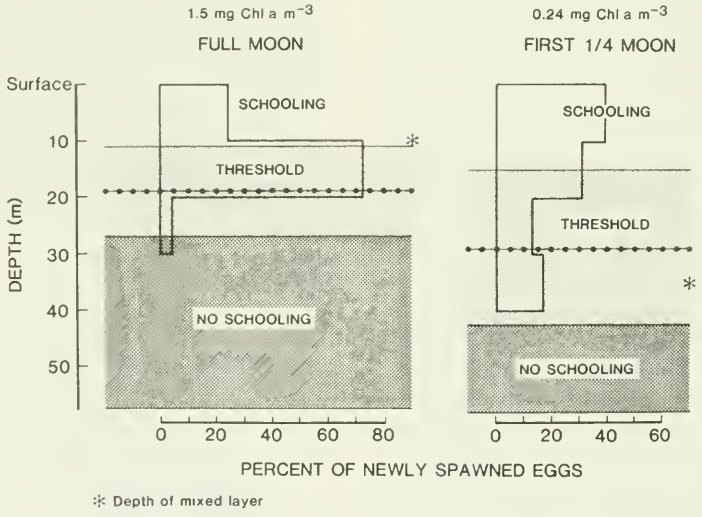

FIGURE 4.—Comparisons of the estimated depths of schooling of northern anchovy and the observed depths of spawning. Estimated depth of schooling calculated from visual threshold estimates (W $cm^{-2}_{anch.\ eff.}$), an assumed dissolved organic matter of 0.7 mg l^{-1}, and the average Chl a concentration and moon phase at the station (1/4 moon phase assumed to be equivalent to starlight) using the model of Baker and Smith (1982). Observed spawning depths at the two stations are indicated by a frequency histogram for newly spawned anchovy eggs where the y axis indicates the depth stratum of the plankton tow and the x axis indicates the percentage of newly spawned eggs taken at each of the 10 m vertically stratified tows. Data are from Pommeranz and Moser (1980) and are for the total number of newly spawned eggs taken over a 4-8 d interval.

TABLE 3.—Upper and lower bound and geometric mean for the visual threshold for schooling of adult northern anchovy, *Engraulis mordax*, in the various energy units.

Energy units	Schooling[1]	No schooling[2]	Geometric mean[3]
Radiometric ($W\ cm^{-2}$)	4.777×10^{-10}	7.785×10^{-12}	6.051×10^{-11}
Anchovy effective[4] ($W\ cm^{-2}_{anch.\ eff.}$)	3.079×10^{-10}	5.018×10^{-12}	3.900×10^{-11}
Photometric[5] (mc)	2.048×10^{-3}	3.337×10^{-5}	2.594×10^{-4}

[1]Lowest irradiance level at which schooling occurred.
[2]Highest irradiance level at which anchovy failed to school.
[3]Geometric mean of the irradiance at the upper and lower bounds of the threshold.
[4]Weighted by ERG action spectra for *Engraulis encrasicholus* dark adapted retina (413-612 nm) (Protasov 1964).
[5]Weighted by the 1964 human photopic response (413-600 nm).

than that for jack mackerel (3.5×10^{-5} mc, Hunter 1968), a species associated with anchovy in the California Current. Visual thresholds for schooling in fishes range from about 1×10^{-5} to 1×10^{-1} mc with about 90% (14/16) of the literature values being higher than anchovy (Blaxter 1970). We do not attach much importance to such specific differences because criteria for schooling differ widely and radiometric procedures in the older studies were primitive by today's standard. We suspect the threshold for jack mackerel may have been lower than the northern anchovy because of use of a uniform and highly reflective background in the apparatus and the use of photometric brightness as a unit of measurement. In our work the brightness to the sides and below was much lower than the downwelling irradiation whereas this was not the case in the jack mackerel experiment.

ACKNOWLEDGMENTS

We thank Mike Sokol (Southampton College, NY) for constructing the apparatus and for conducting some of the experiments and Sandor Kaupp (University of California at San Diego) who provided advice and assistance throughout the study. We also thank Tilman Pommeranz and Geoffrey Moser for permitting us to use their unpublished data on vertical distribution of anchovy eggs, and Paul Smith, Tilman Pommeranz, Roger Hewitt, and J. H. S. Blaxter for reviewing the manuscript.

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DISTRIBUTIONAL PATTERNS OF FISHES CAPTURED ABOARD COMMERCIAL PASSENGER FISHING VESSELS ALONG THE NORTHERN CHANNEL ISLANDS, CALIFORNIA

MILTON S. LOVE,[1] WILLIAM WESTPHAL,[1] AND ROBSON A. COLLINS[2]

ABSTRACT

We surveyed fishes taken aboard commercial passenger fishing vessels along the four northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) within the Southern California Bight. Fourteen species declined in abundance along the Northern Channel Island chain. Colder water forms decreased to the east, while temperate species declined to the west. In the shallowest depth interval (0-36 m), the mean lengths of four rockfish species increased toward the west. In general, the size of these four species also increased with depth. We believe these phenomena are linked to the differences in water temperature between the islands—with cold, California Current water dominant in the west, and warmer Southern California Bight water entrained in the east.

The mainland coast of California is distinguished by two faunal provinces: A warm-temperate Californian Province lies south of Point Conception and a cold-temperate Oregonian Province exists to the north (Seapy and Littler 1980). In shallow waters, the fish fauna of the Californian Province is a mixture of eurythermic temperate and subtropical species, while the Oregonian Province is predominantly a colder temperate region, with few subtropical species present.

Recent studies examining the distributional patterns of marine intertidal invertebrates (Littler 1980; Seapy and Littler 1980), algae (Murray et al. 1980), and seabirds (Hunt et al. 1980) around southern California islands imply there is a replication of these two mainland faunal provinces along the 88 km, east-west lying, northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa) (Fig. 1). Oregonian Province species dominate the western end of the chain, while the fauna of the eastern end is more Californian.

There is little published on the biogeography of fishes around the northern Channel Islands. Ebeling et al. (1980a, b) examined the fish populations of Santa Cruz Island kelp beds, and Hubbs (1967, 1974) stated that the fish communities of San Miguel were closely related to those of central California, while about Santa Cruz fish were typical of southern California. No other work has been published on this topic.

In this paper, we describe one aspect of the northern Channel Islands' fish fauna, utilizing data gathered by the California Department of Fish and Game in their Commercial Passenger Fishing Vessel creel census. This census (fully described in Methods) counted, measured, and noted the location and depth of capture of fishes taken by hook and line on sportfishing passenger vessels in southern California.

Data from this study could not give an unbiased estimate of species composition. Most angling involved fishing with live bait (primarily northern anchovies, *Engraulis mordax*) or with lures simulating fishes, and angling techniques were similar along the island chain. Thus, the sample was biased toward relatively large-mouthed, piscivorous species. However, the purpose of this study was to ascertain distributional patterns of whatever species were taken by these methods, rather than attempting to describe entire fish communities.

METHODS

Fishes taken aboard commercial passenger fishing vessels (CPFV) were sampled by the senior author and by California Department of Fish and Game personnel from April 1975 to December 1978. The sampling units (trips) were chosen randomly, and the population sampled consisted of all regularly scheduled trips by CPFV's operating south of Point Conception to the Mexican border.

The sampler assigned to each boat boarded the

[1]VANTUNA Research Group, Moore Laboratory of Zoology, Occidental College, Los Angeles, CA 90041.
[2]Marine Resources Branch, California Department of Fish and Game, 1301 W. 12th, Long Beach, CA 90813.

Manuscript accepted August 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

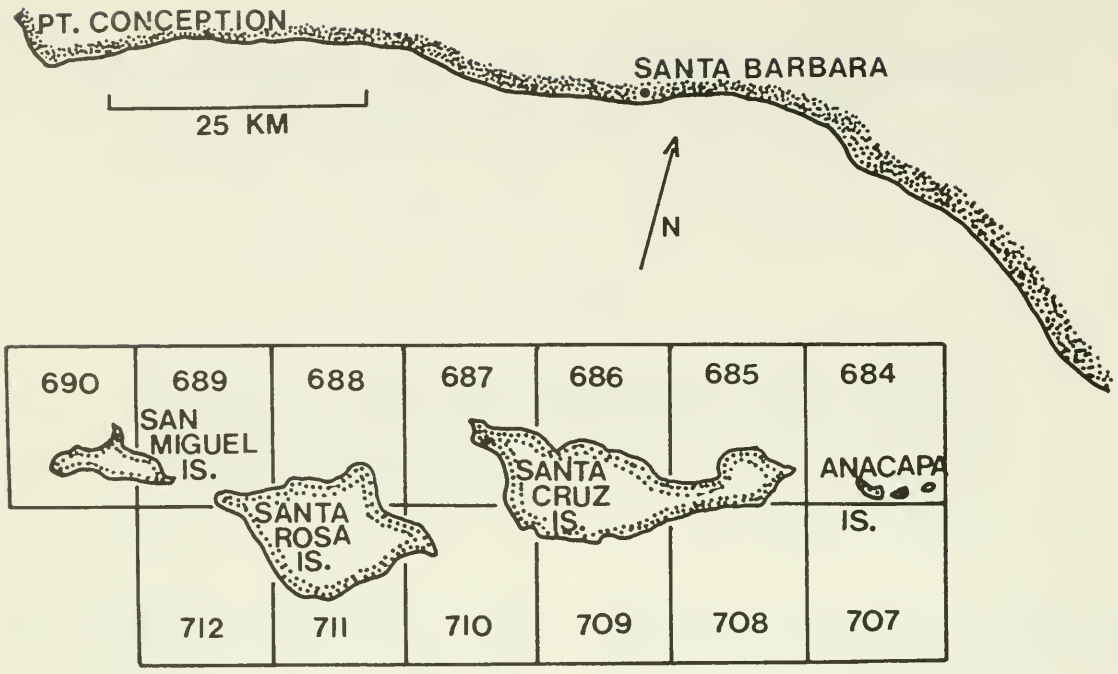

FIGURE 1. – Location and block numbers of sampling sites about the northern Channel Islands, CA.

boat at the beginning of the trip and remained aboard, measuring and identifying all fish caught by the passengers, until the boat returned to dock. A particular effort was made to measure every fish landed, even those returned alive to the water because of undesirability or in compliance with bag or size limit regulations. Also noted were the number of anglers aboard the vessel, the hours of fishing, and the location and depth of fishing effort.

Each fish was placed on a plastic measuring sheet held in a two-sided aluminum frame and the length marked. Total length (tip of snout to tip of depressed caudal fin) was recorded for all fish except members of the jack (Carangidae) and mackerel (Scombridae) families, from which fork length was taken.

A portion of the caudal fin was clipped from each fish measured so that the fish could be recognized later. When fish were brought aboard too rapidly for all to be measured, samplers gave immediate priority to those being returned to the water and measured the remaining fish at the end of fishing or during a break in activity. When samplers were uncertain of the identification of a fish, they retained it for positive identification. After completing a trip, the samplers tallied and recorded by species the data collected. Individual fish lengths were measured on the plastic sheet with a meter stick.

The California Department of Fish and Game has divided marine waters off California into numbered blocks. For this study, we utilized data from block numbers 684-690 and 707-712 (Fig. 1). Care was taken to remove data from mainland fishing sites in block number 684. Block 710 was Santa Rosa Island alone.

We measured fish abundances by catch per unit effort, which was defined as number of fish taken per angler hours (where angler hours = number of anglers × number of hours fished).

RESULTS

One hundred and nineteen trips were made, and the catches from 3,712 anglers were sampled. A total of 23,089 fishes of 78 species were tallied, of which 49 are listed in Table 1. Rockfishes (particularly bocaccio, *Sebastes paucispinis*; blue rockfish, *S. mystinus*; and olive rockfish, *S. serranoides*) and kelp bass, *Paralabrax clathratus*, were numerically dominant. Among the 20 most abundant species, only 4 (*Paralabrax clathratus*; chub mackerel, *Scomber japonicus*; lingcod, *Ophiodon elongatus*; ocean whitefish, *Caulolatilus princeps*) were not rockfishes.

We stratified our data by depth (36 m intervals).

TABLE 1.—Partial list of fishes taken aboard commercial passenger fishing vessels during sampling from April 1975 to December 1978 around the northern Channel Islands. Only those species where 10 or more individuals were taken are listed.

Sebastes paucispinis	3,183
Sebastes mystinus	3,074
Paralabrax clathratus	2,985
Sebastes serranoides	2,632
Sebastes goodei	1,619
Sebastes atrovirens	1,509
Sebastes miniatus	1,119
Sebastes caurinus	1,069
Scomber japonicus	671
Sebastes chlorostichus	632
Sebastes rufus	491
Sebastes carnatus	409
Sebastes entomelas	372
Sebastes constellatus	332
Ophoidon elongatus	304
Sebastes rosaceus	296
Sebastes ovalis	235
Caulolatilus princeps	215
Sebastes levis	197
Sebastes elongatus	195
Sebastes auriculatus	156
Sebastes rosenblatti	148
Semicossyphus pulcher	142
Sebastes rubrivinctus	121
Sebastes eos	120
Sebastes hopkinsi	105
Sebastes chrysomelas	102
Scorpaena guttata	60
Sebastes serriceps	54
Medialuna californiensis	49
Sebastes pinniger	46
Sebastes rastrelliger	43
Genyonemus lineatus	36
Sarda chiliensis	33
Eopsetta jordani	32
Sebastes gilli	21
Sphyraena argentea	20
Citharichthys sordidus	19
Scorpaenichthys marmoratus	19
Trachurus symmetricus	19
Sebastes simulator	18
Chromis punctipinnis	17
Prionace glauca	17
Seriola lalandei	17
Sebastes ensifer	15
Seriphus politus	15
Sebastes nebulosus	12
Paralichthys californicus	10
Sebastes ruberrimus	10

As virtually all fishing effort in waters deeper than 72 m was carried out in the eastern part of the chain, no analyses were conducted of catches in these depths. Most species' abundance trends occurred in the shallowest (0-36 m) depth interval. No samples in 0-36 m were taken in blocks 688, 689, and 709, and none in 37-72 m in blocks 690, 709, 720, 411, and 712.

Fourteen species (Table 2) decreased in abundance along the island chain in 0-36 m (Table 3, Kolmogorov-Smirnov goodness of fit test). Of these, eight species (*Ophiodon elongatus*; *Paralabrax clathratus*; Pacific bonito, *Sarda chiliensis*; *Scomber japonicus*; China rockfish, *Sebastes nebulosus*; yellowtail, *Seriola lalandei*; Pacific barracuda, *Sphyraena argentea*; jack mackerel, *Trachurus symmetricus*) were absent around either the extreme eastern or western end of the chain. The abundance of seven species (*Paralabrax clathratus*, *Sarda chiliensis*, *Scomber japonicus*, *Scorpaena guttata*, *Seriola lalandei*, *Sphyraena argentea*, *Trachurus symmetricus*) decreased toward the west and seven (*Ophiodon elongatus*; copper rockfish, *Sebastes caurinus*; *S. miniatus*; *S. mystinus*; *S. nebulosus*; *S. paucispinis*; *S. serranoides*) decreased toward the east.

The catch per unit effort (CPUE) of six species (*Ophiodon elongatus*, *Sebastes caurinus*, *S. miniatus*, *S. mystinus*, *S. paucispinis*, *S. serranoides*) increased in the next (37-72 m) depth interval (Table 4). The largest increases occurred around Anacapa (blocks 684, 707) and the eastern end of Santa Cruz (685, 708). In most instances, catches increased by a factor of 10 or more in these four blocks. The CPUE of three species (*Sebastes miniatus*, *S. serranoides*, and *S. paucispinis*) were over 100× as great in several blocks.

There was a cline in the mean lengths of four species (*Sebastes caurinus*, *S. mystinus*, *S. paucispinis*, *S. serranoides*) in the shallowest depth interval along the island chain (Fig. 2). All four species were largest in the shallow waters of the more westerly islands, particularly San Miguel.

We compared mean lengths of each species between blocks within the 0-36 m and 37-75 m depth intervals using the Student-Newman-Keuls multiple range test (Sokal and Rohlf 1969). In the shallowest interval, *Sebastes caurinus*, *S. mystinus*, and *S. serranoides* were largest off San Miguel, while *S. paucispinis* lengths were greatest at San Miguel and Santa Rosa. Two groupings, San Miguel-Santa Rosa and Santa Cruz-Anacapa, were evident in three species (*Sebastes mystinus*, *S. paucispinis*, *S. serranoides*) as mean lengths of these tended to form somewhat discrete units. For *Sebastes caurinus*, San Miguel, Santa Rosa, and the west end of Santa Cruz formed one entity – eastern Santa Cruz and Anacapa another.

For these four species, mean lengths were, in most instances, greater in each block in deeper (37-75 m) waters. Though some of the groupings of 0-36 m existed, there was some breakdown of this pattern. In *Sebastes paucispinis*, for instance, the mean lengths of Santa Rosa (block 688) and Anacapa (707) fish were similar, though they were different in 0-36 m.

TABLE 2.—Catch per unit effort × 100, of 14 species taken about the northern Channel Islands in 0-36 m. Block numbers are arranged approximately west to east. The unit of effort is number of fish taken per angler hours (where angler hours = number of anglers × number of hours fished). tr = < 0.01.

Blocks:	690	712	711	710	687	686	685	708	684	707
Ophiodon elongatus	1.1	0.80	0.41	0.23	0.33	0.02	0.03	0.03	tr	0.09
Paralabrax clathratus	0.0	3.62	7.10	0.78	2.65	31.85	2.97	68.33	2.11	22.10
Sarda chiliensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06	0.0
Scomber japonicus	0.02	0.0	0.0	0.97	0.52	0.0	0.21	15.00	0.43	16.88
Scorpaena guttata	0.01	0.0	0.0	0.07	0.0	0.0	0.04	0.03	0.05	1.17
Sebastes caurinus	2.84	7.63	29.68	1.19	1.31	1.45	0.34	0.53	0.16	0.26
Sebastes miniatus	2.92	1.30	0.31	1.26	0.0	0.0	0.04	0.01	tr	0.86
Sebastes mystinus	9.70	17.01	8.85	16.05	3.06	7.61	3.00	1.02	0.21	8.51
Sebastes nebulosus	2.08	2.07	0.36	0.86	0.0	0.0	0.06	0.0	0.03	0.82
Sebastes paucispinis	0.06	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sebastes serranoides	21.31	42.72	16.09	0.69	1.56	3.46	0.41	0.63	0.19	0.86
Seriola lalandei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.92
Sphyraena argentea	0.0	0.0	0.0	0.0	0.14	0.0	0.0	0.0	tr	tr
Trachurus symmetricus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.03	0.0

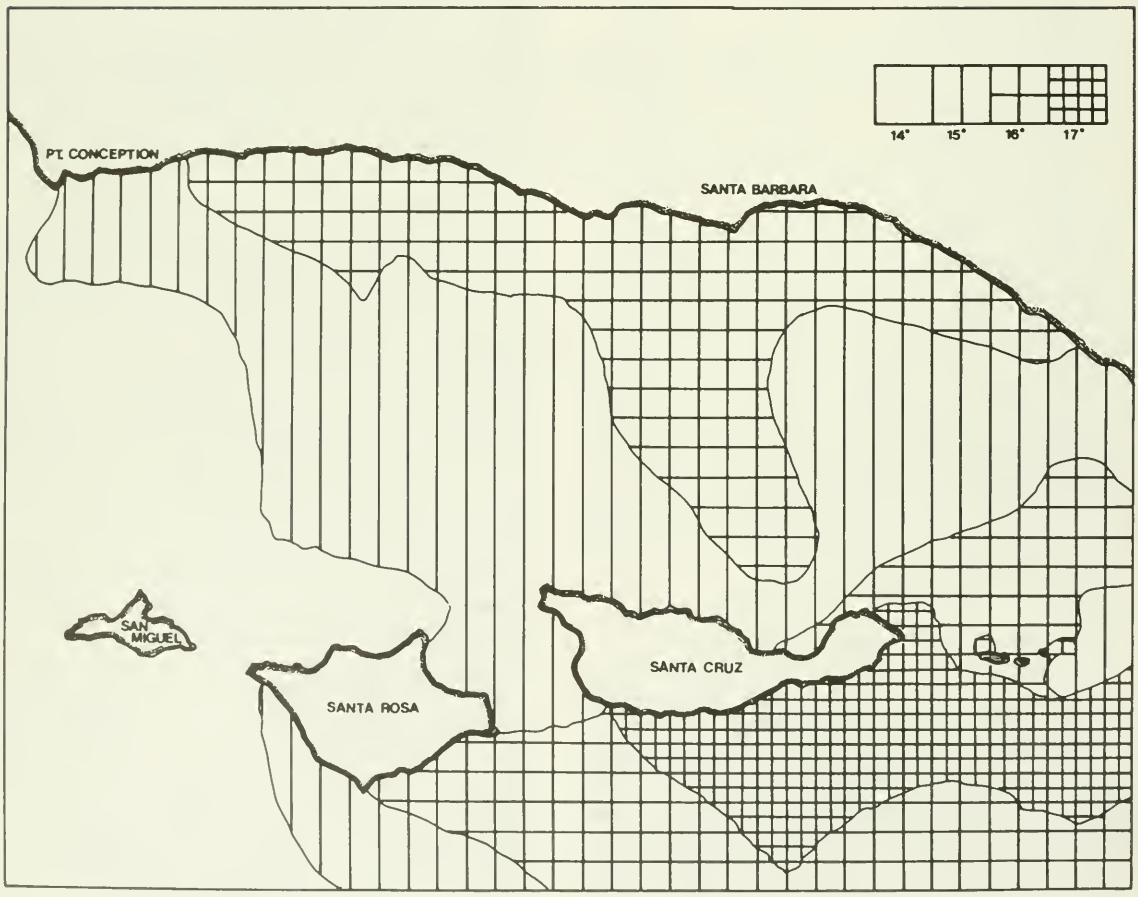

FIGURE 2.—Mean lengths of four species in two depth intervals (0-36 m and 36-76 m) captured along the northern Channel Islands. Dots represent means; bars represent 95% confidence intervals.

TABLE 3.—Fourteen species demonstrating significant catch per unit effort trends (Kolmogorov-Smirnov goodness of fit test) along the northern Channel Islands in 0-36 m.

	Z	P
Ophiodon elongatus	1.64	0.009
Paralabrax clathratus	1.89	0.002
Sarda chiliensis	2.72	< 0.001
Scomber japonicus	1.72	0.002
Scorpaena guttata	2.39	< 0.001
Sebastes caurinus	2.24	< 0.001
Sebastes miniatus	1.57	0.014
Sebastes mystinus	2.10	< 0.001
Sebastes nebulosus	2.69	< 0.001
Sebastes paucispinis	1.49	0.024
Sebastes serranoides	1.97	0.001
Seriola lalandei	2.52	< 0.001
Sphyraena argentea	1.92	0.001
Trachurus symmetricus	2.43	< 0.001

proximity to Point Conception and to the California Current (Reid et al. 1958; Neushul et al. 1967; Kolpack 1971; Seapy and Littler 1980). At Point Conception, as the land extends eastward, the cold California Current continues flowing southward. As it flows offshore, the eastern edge surrounds San Miguel Island and some water spills into the Santa Barbara Channel, flowing along the northern sides of Santa Rosa and Santa Cruz Islands (slowly warming as it travels). Much of the California Current continues to flow southeastward and is later entrained in a slow-moving and warm counterclockwise eddy (Southern California Eddy) within the Southern California Bight. Areas influenced by this eddy, such as Anacapa Island, the southern sides of Santa Rosa and Santa Cruz Islands, and, to a certain extent, the

TABLE 4.—Comparison of catch per unit effort × 100 of six species between two depth intervals (0-36 m and 37-72 m). Block numbers are arranged approximately west to east.

		Blocks										
	Depth	690	688	712	711	710	687	686	685	708	684	707
Ophiodon elongatus	0-36	1.1	—	0.80	0.41	0.23	0.33	0.02	0.03	0.03	tr[1]	0.09
	37-72	—	100.02	—	—	—	1.14	—	0.08	1.53	4.08	0.38
Sebastes caurinus	0-36	2.84	—	7.63	29.68	1.19	1.31	1.45	0.34	0.53	0.16	0.26
	37-72	—	33.28	—	—	—	6.41	—	0.92	8.36	7.68	3.61
Sebastes miniatus	0-36	2.92	—	1.30	0.31	1.26	0.0	0.0	0.04	0.01	tr[1]	0.86
	37-72	—	12.41	—	—	—	6.25	—	0.29	2.04	3.61	0.68
Sebastes mystinus	0-36	9.70	—	17.01	8.85	16.05	3.06	7.61	3.00	1.02	0.21	8.51
	37-72	—	17.08	—	—	—	12.77	—	5.28	16.92	57.21	7.41
Sebastes paucispinis	0-36	2.08	—	2.07	0.36	0.86	0.0	0.0	0.06	0.0	0.03	0.82
	37-72	—	18.21	—	—	—	13.81	—	0.54	10.21	22.81	10.25
Sebastes serranoides	0-36	21.31	—	42.72	16.09	0.69	1.56	3.46	0.41	0.63	0.19	0.86
	37-72	—	4.11	—	—	—	1.63	—	2.89	2.91	22.81	0.28

[1]tr = < 0.01.

Similarly, the distinctions between mean lengths of *S. serranoides* in 0-36 m off Santa Rosa versus Anacapa were not evident in 37-75 m. There was no difference in *S. mystinus* mean lengths between Santa Rosa, Santa Cruz, and Anacapa.

DISCUSSION

Temperature Regime

Previous studies indicate that temperature plays a major role in the community structure of invertebrates and algae along the northern Channel Islands (Littler 1980; Murray et al. 1980; Seapy and Littler 1980), and water temperature was correlated with patterns we observed in fish species abundances and size frequencies. Water temperatures surrounding these islands are strongly influenced by their relative northern sides of Santa Rosa and Santa Cruz, are warmer than areas bathed by the California Current alone. Surface water temperature differences may be as much as 12°C between San Miguel and Anacapa, and 8°C between the west end of Santa Cruz and Anacapa (Hubbs 1967).

Figure 3 exemplifies this condition. It represents the mean of surface temperatures observed by the NOAA-7 satellite on 8 d throughout 1981[3]. Though 1981 was a relatively warmwater year within the Southern California Bight, the influence of the California Current is plain around San Miguel, much of Santa Rosa, and the western end of Santa Cruz Islands. Warm water from southern California bathes southern and eastern Santa Cruz and the

[3]Data taken from observations on 29 January, 15 February, 22 March, 16 May, 4 August, 30 September, 11 October, and 25 November 1982.

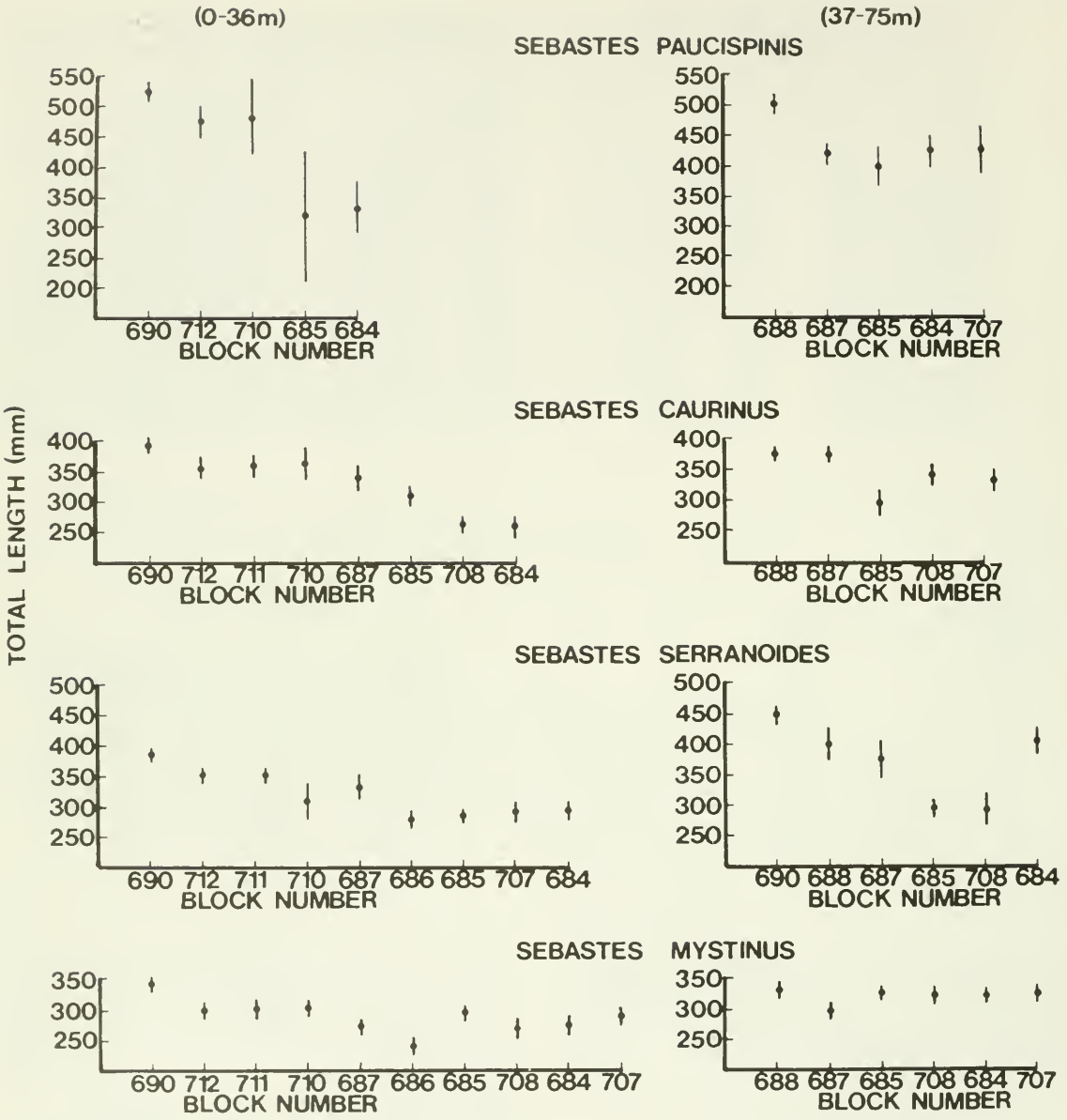

FIGURE 3.—Mean surface temperatures about the northern Channel Islands, based on 8 d throughout 1982 (see text footnote 3).

southeastern corner of Santa Rosa Islands. Warm water occurred close to shore around Anacapa Island, while cooler (perhaps upwelled) conditions occurred slightly offshore to the east.

Fish Distribution

Data from our study suggest that the fish communities of the northern Channel Islands resemble those of the central and southern California mainland. San Miguel and Santa Rosa harbor a more temperate fauna than Santa Cruz and Anacapa. A number of species characteristic of southern California (i.e., *Sarda chiliensis*, *Scomber japonicus*, *Seriola lalandei*, *Sphyraena argentea*) were not found off San Miguel or Santa Rosa, while other southern California species (*Scorpaena guttata* and *Paralabrax clathratus*) were less abundant around

the western islands. Similarly, fishes more characteristic of the Oregonian Province (*Ophiodon elongatus, Sebastes caurinus, S. nebulosus*) were less abundant or absent off Santa Cruz and Anacapa. Evidence from Miller and Lea (1972) bolsters this impression. Nineteen species have geographic range limits along the island chain; of these, 9 (*Anoplarchus purpurescens, Artedius harringtoni, Chirolophis nugator, Hippoglossus stenolepis, Nautichthys oculofasciatus, Radulinus vinculus, Sebastes nebulosus, Stichaeopsis*? sp., *Synchirus gilli*) are temperate and 10 (*Alloclinus holderi, Caranx caballus, Chaenopsis alepidota, Cryptotrema corallinum, Gibbonsia erythra, Gnathephis catalinensis, Gobiesox rhessodon, Leiocottus hirundo, Mobula japonica, Paraclinus integrippinis*) are subtropical or tropical. With only one exception (*Radulinus vinculus*), species on the list typical of the Oregonian Province have their southern limit about San Miguel or Santa Rosa, while most southern forms are limited to Anacapa and Santa Cruz.

Around Anacapa and the eastern end of Santa Cruz, six species (*Ophiodon elongatus, Sebastes caurinus, S. miniatus, S. mystinus, S. paucispinis, S. serranoides*) found in shallow water (0-36 m) to the west were more abundant over deeper (37-72 m) reefs. This is an example of "isothermic submergence" (Briggs 1974). Discussing the mainland southern California fish fauna, Briggs noted that cooler preferring, temperate species sought deeper, cooler waters in the warmer parts of their ranges. All six species are temperate forms, all are found in shallower waters off central California than along the mainland of the Southern California Bight.

The increased length of four rockfishes (*Sebastes caurinus, S. mystinus, S. paucispinis, S. serranoides*) in shallow water around the western islands is at least partially due to a variant of isothermic submergence. Among rockfishes, juveniles are more eurythermic than adults (Miller and Geibel 1973; Love 1978), favoring shallower, warmer waters. Juveniles of these four species were found in shallow waters along all the islands (though in decreasing abundance toward the warmer east), while adults were abundant in shallow waters only in the cooler, more westerly part of the island chain.

Might the trend toward decreased mean sizes in the eastern section be, in part, due to relatively high fishing pressure? There are no records of total fishing effort, stratified by depth, around these islands. However, the California Department of Fish and Game does have data on total angler-hours within each block, derived from operator log-book records. We present these data for 1975-78 in Table 5. It is

TABLE 5.—Partyboat effort about the northern Channel Islands, 1975-78.

	Year	No. anglers	No. anglers-hours
Block 684	1978	11,129	56,571.5
	1977	3,295	14,743.4
	1976	6,152	27,250.5
	1975	7,465	35,296.5
			133,861.9
Block 685	1978	3,048	14,596.0
	1977	2,765	13,951.4
	1976	4,689	23,135.5
	1975	7,088	32,997.9
			84,680.8
Block 686	1978	951	4,588.0
	1977	1,044	5,293.9
	1976	1,500	7,941.0
	1975	2,504	11,803.2
			29,626.1
Block 687	1978	947	4,534.0
	1977	1,213	6,400.0
	1976	2,115	9,928.0
	1975	3,193	16,016.5
			36,878.5
Block 688	1978	1,397	6,723.4
	1977	1,363	6,838.5
	1976	2,745	15,161.5
	1975	2,840	15,425.0
			44,148.4
Block 689	1978	1,259	5,986.4
	1977	1,318	6,423.0
	1976	1,951	9,193.5
	1975	1,692	7,795.5
			29,398.4
Block 690	1978	4,732	19,885.3
	1977	5,065	23,292.7
	1976	6,204	27,576.5
	1975	6,565	28,374.0
			99,128.5
Block 707	1978	3,994	19,580.6
	1977	1,498	7,297.0
	1976	877	3,974.5
	1975	2,448	11,636.5
			42,488.6
Block 708	1978	4,650	23,008.0
	1977	5,931	28,793.8
	1976	2,701	13,807.4
	1975	2,202	10,268.0
			75,877.2
Block 709	1978	1,615	7,796.0
	1977	582	2,975.5
	1976	499	2,208.0
	1975	1,129	6,229.0
			19,208.5
Block 710	1978	5,556	24,435.0
	1977	2,800	13,792.5
	1976	1,019	4,964.4
	1975	2,390	12,544.0
			55,735.9
Block 711	1978	764	3,661.5
	1977	1,264	6,528.0
	1976	556	2,459.0
	1975	739	3,530.0
			16,178.5

our experience that much of the fishing effort in these blocks is in the two depth regimes discussed here. Thus we believe the figures in Table 5 are reflective of the relative fishing effort between blocks.

The data indicate that Anacapa (blocks 684, 707) and eastern Santa Cruz (blocks 685, 708) were indeed among the most heavily fished areas. On the other hand, the westernmost section of San Miguel (block 690), with generally the largest fish size frequencies, was also fished intensively. There are other discrepancies between fishing pressure and size frequencies (Fig. 2). Though block 686 (mid-Santa Cruz) is only moderately fished, *Sebastes serranoides* mean lengths (0-36 m) are similar to those of the more heavily impacted areas to the east. The drop in *S. mystinus* length (0-36 m) begins in block 687 (western Santa Cruz), another moderately fished site. In fact, both *S. mystinus* and *S. caurinus* taken in adjacent block 710 (eastern Santa Rosa) are larger than block 687, even though more fishing took place in block 710. This is not to imply that differences in fishing effort between areas may not play a role. Rather, we believe that the response to temperature by these species is also important.

The marine fauna of the Southern California Bight is notable for its temporal fluctuation. Studies of both fossil (Fitch 1969) and present day records (Hubbs 1948; Radovich 1961; Stephens et al. in press) indicate considerable fluctuation in relative abundance between temperate and tropically derived species. Much of this faunal variability is due to unstable water temperature patterns over the continental shelf. Weakening of the California Current allows for a northerly flow of subtropical water and its associated fauna. During periods of strong California Current, temperate forms increase in abundance. Data for this paper were gathered during the end of a cold cycle (1976) and the beginning of a warm one (which continues to the present–1984).

Juveniles and adults may move with insurgent water masses. This is particularly true of such pelagic or semipelagic species as *Seriola lalandei*, *Sphyraena argentea*, *Sarda chiliensis*, and *Scomber japonicus*. All occur about Santa Cruz and Anacapa Islands (and throughout much of the Southern California Bight) in warmwater periods. During the strong 1983 El Niño, the tropical yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Euthynnus pelamis*, ventured far north of their usual range up to Santa Cruz Island. Even relatively sedentary species may follow currents. The finescale triggerfish, *Balistes polylepis*, was an early migrant into southern California at the beginning of the warm cycle in the mid-1970's and remains relatively common about inshore reefs as far north as Santa Barbara.

Larval transport and subsequent species recruitment may be affected by changes in water masses. During 1983, a number of warm-temperate species (including rock wrasse, *Halichoeres semicinctus*; garibaldi, *Hypsypops rubicunda*; spotted sandbass, *Paralabrax maculatofasciatus*; *Seriola lalandei*; *Sphyraena argentea*; salema, *Xenistius californiensis*) recruited off Santa Barbara, well north of their usual range.[4] Similar unusual northerly recruitment of *Semicossyphus pulcher* and Catalina goby, *Lythrypnus dalli*, occurred during the same period off central California.[5]

Young of-the-year of warm-temperate species have recruited north of their usual range in past warm periods, e.g., 1957-58 (Radovich 1961). In many cases, such as that of the opaleye, *Girella nigricans*, off Monterey, only a single year class (i.e., 1958) survives, leading in succeeding years to populations of similar-sized individuals.[6] During the early 1970's, we observed that the population of *Semicossyphus pulcher* around San Miguel, was composed entirely of large individuals. Perhaps these, too, were the survivors of a successful year class during the 1957-58 warmwater period.

Conversely, during the years of strengthened California Current, species more representative of central California recruit south. The early 1970's were a relatively cool water period and temperate species such as kelp greenling, *Hexagrammos decagrammus*; *Ophiodon elongatus*; *Sebastes mystinus*; and *S. serranoides* young-of-the-year successfully recruited in southern California (Stephens and Zerba 1981; Stephens et al. in press). These maintained themselves in the locally cool habitat at the head of Redondo Submarine Canyon, well after they disappeared from much of the Bight. Water temperature is also responsible for the continuation of long-term temperate species remnant populations on the southern sides of several Baja California points (Hubbs 1960). Here, upwelling water creates suitable conditions for a number of temperate species, which are either missing from, or found in deeper water off of, southern California.

[4]S. Anderson and J. McCullaugh, Marine Science Institute, University of California, Santa Barbara, CA 93106, pers. commun. November 1983.

[5]D. Miller, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, pers. commun. January 1977.

[6]F. Henry, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, pers. commun. November 1983.

It is likely that a continuing warmwater regime has or will alter the species' composition we found. For instance, we might expect less successful year classes among the rockfishes about the eastern islands. Stephens et al. (in press) noted the essentially complete failure of *Sebastes mystinus* and *S. serranoides* recruitment off Palos Verdes and Redondo Beach (on the southern California mainland) during this current warmwater cycle. On the other hand, warmwater species, such as *Paralabrax clathratus* or *Scorpaena guttata*, might recruit more successfully around the previously cool westerly islands. Migratory species, such as *Seriola lalandei*, *Sphyraena argentea*, or *Scomber japonicus* may also be more abundant about these westerly islands.

ACKNOWLEDGMENTS

We thank A. W. Ebeling for reviewing an early draft and S. Warschaw for typing the manuscript. J. Svejkovsky (Scripps Institution of Oceanography-Satellite Oceanography) supplied the satellite sea surface temperature data. This work was supported, in part, by Federal Aid to sportfish restoration (Dingell-Johnson) funds.

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MORPHOLOGICAL DEVELOPMENT, IDENTIFICATION, AND BIOLOGY OF LARVAE OF PANDALIDAE, HIPPOLYTIDAE, AND CRANGONIDAE (CRUSTACEA, DECAPODA) OF THE NORTHERN NORTH PACIFIC OCEAN

Evan B. Haynes[1]

ABSTRACT

All published descriptions of pandalid, hippolytid, and crangonid larvae of the northern waters of the North Pacific Ocean are summarized. Included are recent changes in nomenclature, definitions of terms used in describing the larvae, and procedures for preparing larvae for examination. The general morphology of larvae of the three families is reviewed, and development of the morphological characters used for their identification is discussed. Principal morphological characters and number of larval stages of known larvae in each family are tabulated. Pandalid larvae are keyed to species and stage of development. A synopsis of the most important morphological characters used for identification is given for larvae of each family, genus, and species. Biology of the larvae is reviewed.

Larvae of the Pandalidae, Hippolytidae, and Crangonidae (order Decapoda, tribe Caridea) are common inhabitants of the neritic meroplankton of the northern (temperate and arctic) waters of the North Pacific Ocean. About 135 species of shrimps are found in these waters, and larvae have been described, at least in part, for 46 species. Many of these descriptions, especially of hippolytids and crangonids, are scattered in various foreign scientific journals.

This report summarizes the morphology of described larvae of the Pandalidae, Hippolytidae, and Crangonidae of the northern North Pacific Ocean and gives instructions for examining them. Development of the characters used for identification is discussed, and a generalized key to stage is given. Larvae of each family, genus, and species are characterized morphologically, and the principal morphological characters and the number of the larval stage are tabulated. Illustrated keys to species and stages are provided for 9 of the 13 pandalid species recorded from the northern North Pacific Ocean. Descriptions of larvae of the remaining four species of pandalids have not been published although their probable morphology has been discussed (Haynes 1980a). References to the published descriptions of larvae of each species and a review of the biology of the larvae are provided.

In the synopses of species, I have selected the most distinguishing larval characters; however, these characters may not always be repeated for similar species, and additional characters may be needed for a specific diagnosis. Other distinguishing characters for the larvae discussed here can often be found in the original published descriptions.

An annotated listing of published descriptions precedes the synopsis of each species. When two or more descriptions are listed, the most complete description is given first. Whenever a "?" appears after a species name or stage in the listings, the author of the original description was uncertain of the identification. In these cases, references to the corrected or verified identification are included in the listing. For a few species, descriptions of larvae are based on specimens from the Atlantic Ocean. It should be noted that morphological characters of larvae of the same species from different geographical areas may vary somewhat (Haynes 1978a).

Taxonomic Nomenclature

I used Rathbun's (1904) nomenclature of Pandalidae except for *Pandalus tridens*. After considering both the larval and adult morphology of *P. tridens* (see Rathbun 1902), I give this species full specific rank (Butler 1980; Haynes 1980a) rather than subspecific rank as *P. montagui tridens*, a Pacific subspecies of *P. montagui* Leach 1814.

Nomenclature of the Hippolytidae follows Holthuis' (1947) revision of the genus *Spirontocaris* sensu lato. Holthuis' revision, based on adult morphology, has been verified from larval morphology (Pike and Williamson 1961; Haynes 1981).

Nomenclature of the Crangonidae is based on the

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821.

Manuscript accepted August 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

revision by Kuris and Carlton (1977), with one exception. I use only *Crangon*, rather than *Crangon* and *Neocrangon*, because I agree with Butler (1980) and consider Zarenkov's (1965) separation of the genus *Crangon* into two subgenera, *Crangon* s.s. and *Neocrangon*, to be invalid.

The synopsis of characters of *Crangon septemspinosa* larvae also applies to the characters of *C. affinis* larvae. Needler (1941), Kurata (1964b), and Tesmer and Broad (1964) have described these as two species, but according to Makarov (1967), the two species are synonymous. Descriptions of the lar-

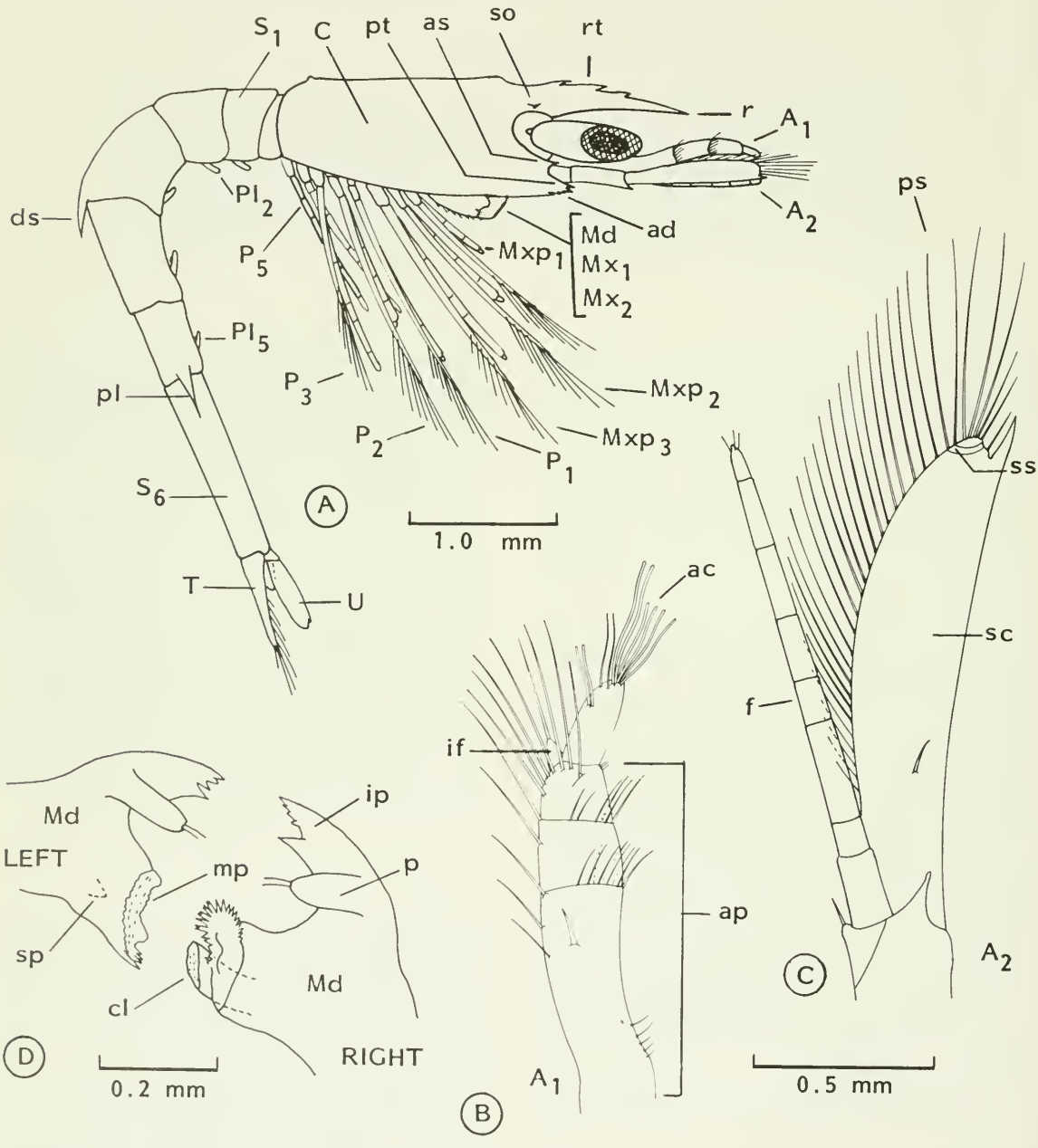

FIGURE 1.—Lateral view and body parts of a diagrammatic decapod shrimp larva. (A) A_1, antennule; A_2, antenna; C, carapace; Md, mandible; Mx_1, maxillule; Mx_2, maxilla; Mxp_1, maxilliped 1; Mxp_2, maxilliped 2; Mxp_3, maxilliped 3; P_1, pereopod 1; P_2, pereopod 2; P_3, pereopod 3; P_5, pereopod 5; Pl_2, pleopod 2; Pl_5, pleopod 5; S_1, somite 1; S_6, somite 6; T, telson; U, uropod; ad, anteroventral denticles; as, antennal spine;

vae of *C. affinis* and *C. septemspinosa* are very similar. More comments on nomenclature for certain species are given in the synopses.

Definition of Terms

I follow Williamson's (1969) terminology for decapod larvae and Haynes' (1979) terminology for larval appendages (Fig. 1). The terms are defined as follows:

abbreviated development – less than five zoeal stages.

carapace length – straight-line distance between the

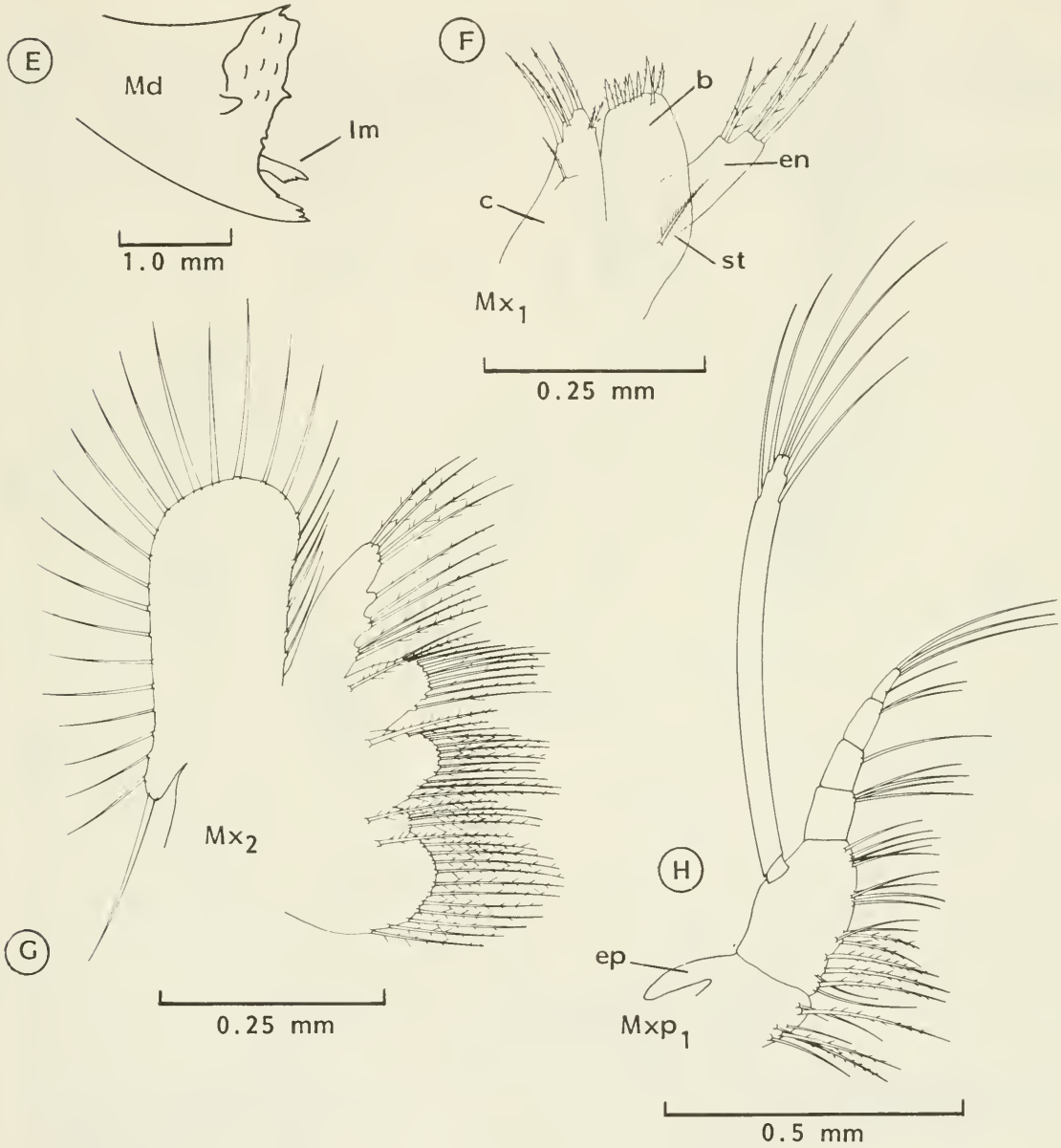

FIGURE 1.–*Continued*–ds, dorsal spine; pl, posterolateral spine; pt, pterygostomian spine; so, supraorbital spine; r, rostrum; rt, rostral teeth. (B) A_1, antennule; ac, aesthetases; ap, antennule peduncle; if, inner flagellum. (C) A_2, antenna; f, flagellum; ps, plumose setae; sc, scale; ss, scale segments. (D) Md, mandible; cl, curved lip; ip, incisor process; mp, molar process; p, palp; sp, subterminal process. (E) Md, mandible; lm, lacinia mobilis. (F) Mx_1, maxillule; b, basipodite; c, coxopodite; en, endopodite; st, subterminal seta. (G) Mx_2, maxilla. (H) Mxp_1, maxilliped 1; ep, epipodite.

posterior margin of orbit and the middorsal posterior margin of the carapace.

denticles – toothlike projections on anteroventral margin of the carapace.

developed pereopods – segmented pereopods directed vertically under cephalothorax.

juvenile – young form, usually small, sexually immature, and generally resembling adult.

larva – a free-swimming phase in the life cycle of the individual whose morphology (such as body form, appendages, and spination) and habit are different from the adult. The term applies to both zoea and

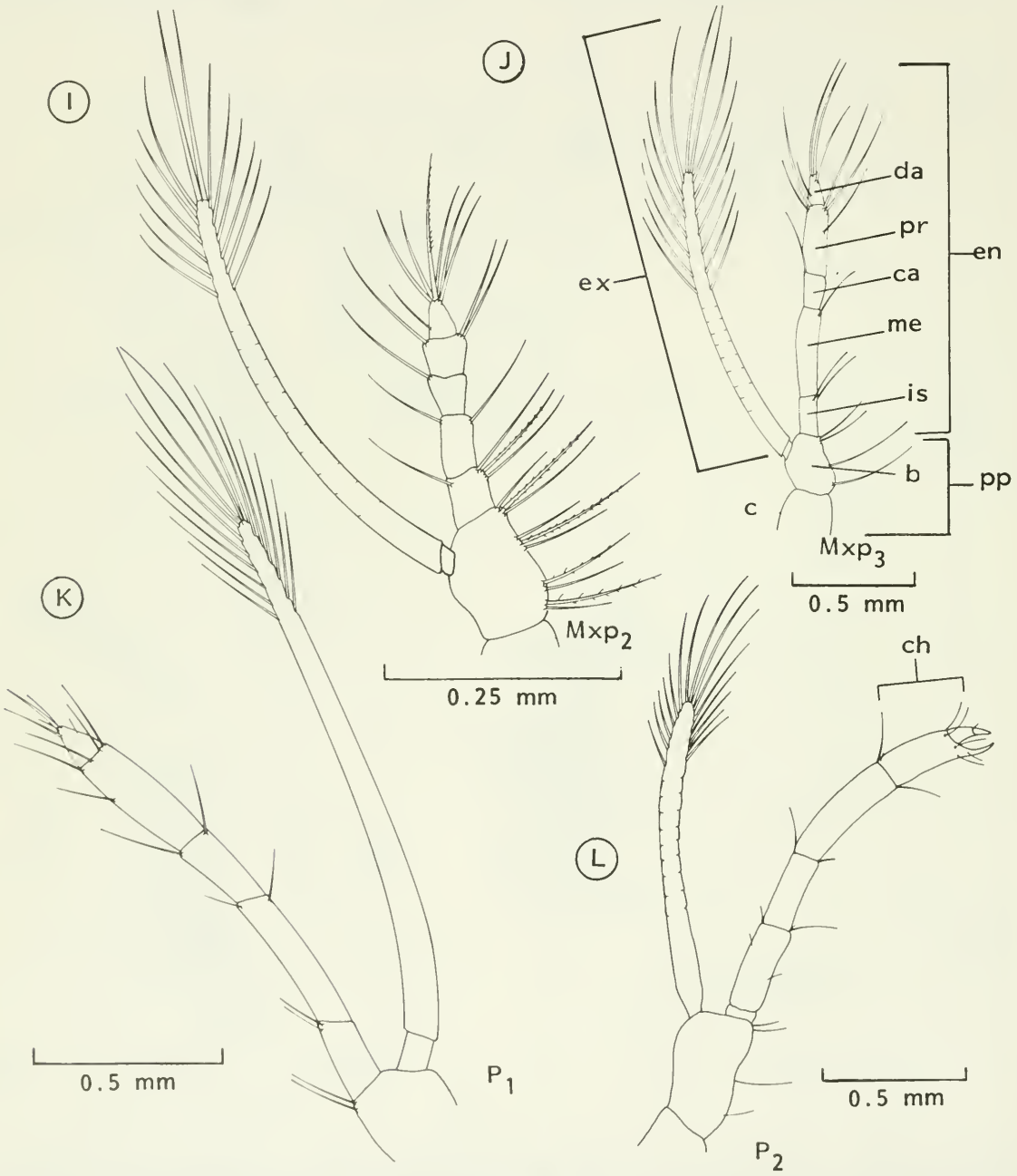

FIGURE 1.–*Continued*–(I) Mxp_2, maxilliped 2. (J) Mxp_3, maxilliped 3; b, basipodite; c, coxopodite; ca, carpopodite; da, dactylopodite; ex, exopodite; en, endopodite, is, ischiopodite; me, meropodite; pp, protopodite; pr, propodite. (K) P_1, pereopod 1. (L) P_2, pereopod 2; ch, chella.

megalopa. (For shrimp, the change from larva to adult is usually somewhat gradual and may include more than one molt.)

megalopa – larva with fully setose natatory pleopods[2] on some or all abdominal somites.

setation formula of telson – setae or spines along the terminal margin of the telson are numbered beginning at the middle of the telson. Thus, 7 + 7 means that the telson has seven pairs of setae along the terminal margin. The first pair is the medial pair.

setose – having setae (bristles).

spine – a sharp, pointed projection, usually long and narrow.

spinose – with many spines.

spiniform – shaped like a spine.

spinule – small spine.

spinulose – with small spines.

stage – intermolt.

subchelate – the dactylopodite (finger) folds against the preceding segment (propodite), as in the first pereopod of crangonid adults.

length – total body length: distance (mm) from the anterior tip of the rostrum to the posterior tip of

[2]In the Decapoda, the development of setose pleopods does not always provide a convenient and clear distinction between zoeal and postzoeal stages. Several species of Pandalidae metamorphose gradually into the postzoeal stage (see Haynes 1976). The term "megalopa", therefore, may include a single stage or several stages depending upon the species. In this paper, the number of larval stages includes all stages before the juvenile stage, regardless of whether the megalopa has one or more stages.

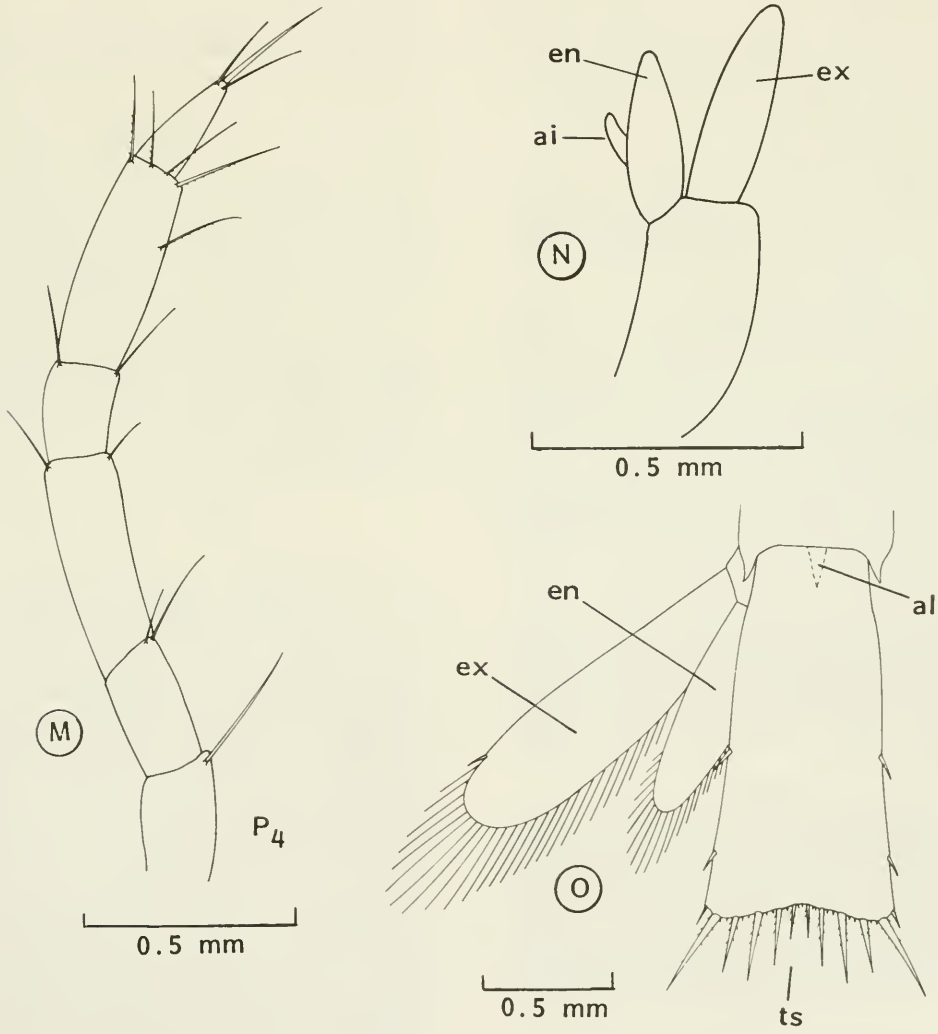

FIGURE 1.–*Continued*–(M) P_4, pereopod 4. (N) Pleopod; ai, appendix interna; en, endopodite; ex, exopodite. (O) Tail fan; al, anal spine; en, endopodite; ex, exopodite; ts, telsonic spines.

telson, excluding telsonic setae or spines.
unabbreviated development – five or more zoeal stages.
undeveloped pereopod – unsegmented pereopod directed anteriorly under cephalothorax.
zoea – larva with natatory setae on maxillipeds, without setose natatory pleopods on some or all abdominal somites 1-5.

Examination Procedure

It is usually necessary to dissect the animal and mount certain appendages on a slide before the identification characters can be used. Visibility of segmentation is often improved by clearing specimens for several days in 10% KOH or full-strength lactic acid. Larvae can be dissected with pins designed for mounting small insects. (The pins are available from most biological supply companies.) After dissecting the larva, place the appendage in a drop of mounting medium (I use Turtox[3] CMC red mounting medium) and cover with a cover glass. Gently press the cover glass to splay hairs and setae and make them easier to examine and count. After mounting the appendages, examine them using a dissecting microscope.

GENERAL MORPHOLOGY OF LARVAE

Pandalid, hippolytid, and crangonid larvae have three major body regions (Fig. 1): head, thorax, and abdomen. The head and thorax are coalesced and are dorsally covered by a common, unjointed cephalothoracic shield, the carapace. The body is divided into 19 true somites which, with their appendages (Fig. 1), are grouped as follows:

1) The head, five indistinguishable fused somites, is covered by the anterior portion of the carapace (C) and has the first five pairs of appendages: antennules (or first antennae) (A_1), antennae (A_2), mandibles (Md), maxillules (Mx_1), and maxillae (Mx_2).
2) The thorax is composed of eight somites that are dorsally fused with, and covered by, the carapace. Each somite has a pair of appendages: Somites 1-3 each have a pair of maxillipeds (Fig. 1A, Mxp_{1-3}); somites 4-8 each have a pair of pereopods (Fig. 1A, P_{1-5}).
3) The abdomen is composed of six somites (Fig. 1A, S_{1-6}) and a terminal segment, the telson (T). The first five somites each have a pair of pleopods (Fig. 1A, Pl_{2-5}). The sixth somite has uropods (U). The uropods, when present with the telson, comprise the tail fan.

CHARACTERS USEFUL FOR IDENTIFICATION OF LARVAE

Understanding the development of morphological characters is necessary for identifying genus, species, and stage of larval development. The following discussion emphasizes the characters most useful for identification. It should be noted, however, that these characters are based on relatively few species of a limited number of genera. For instance, in the family Hippolytidae, the subterminal seta is apparently absent in larvae of *Hippolyte clarki* from British Columbia (Needler 1934) but present in larvae of *H. inermis* and *H. varians* from European waters (Williamson 1957a). The seta may also be present in undescribed *Hippolyte* larvae from the northern North Pacific Ocean. Characterization of the family Pandalidae is based on only two genera, *Pandalopsis* and *Pandalus*. In the northern North Pacific Ocean, described larvae of these two genera develop exopodites only on pereopods 1-2 or 1-3, never on pereopods 1-4. Other genera of the family (e.g., *Plesionika*) may develop exopodites on pereopods 1-4 (Williamson 1957b). Additional descriptions of decapod larvae from the northern North Pacific Ocean will undoubtedly modify the morphological characterizations given here.

Rostrum

In pandalid larvae, the rostrum (Fig. 1A, r) is always long (at least one-third the carapace length). For most species of Pandalidae, the rostrum is styliform in Stage I and does not have teeth (Fig. 1A, rt) until about Stage III. The exceptions are *Pandalopsis coccinata*, *P. dispar*, and *Pandalus platyceros*. In these species, the rostrum is curved in Stage I and has teeth in all larval stages (Berkeley 1930; Kurata 1964a; Price and Chew 1972). In Stage I *Pandalus prensor*, the rostrum curves ventrally between the eyes (Mikulich and Ivanov 1983).

The rostrum of hippolytid larvae may be absent, or, if present, from minute to long. The rostrum is usually without dorsal or ventral teeth in all stages. European specimens of *Eualus gaimardii*, an exception, have two dorsal rostral teeth in the last zoeal stage (Stage V) (Pike and Williamson 1961). If the rostrum is short to long in Stage I, it is also styliform, except in Stage I *Lebbeus groenlandicus* (Fig.

[3]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

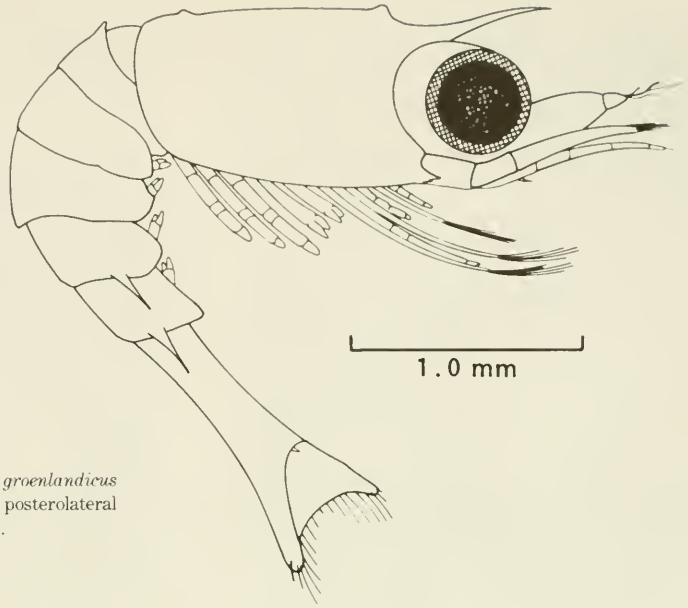

FIGURE 2.–Stage I zoeae of *Lebbeus groenlandicus* showing slightly sinuous rostrum and posterolateral spines on abdominal somites 4 and 5.

2) and *L. polaris*, which have a slightly curved rostrum (Haynes 1978b, 1981). In Stage I *Heptacarpus camtschaticus*, the rostrum is minute and curves slightly downward following the dorsal contour of the eyes (Haynes 1981).

In crangonid larvae, the rostrum is long, spiniform, and without teeth in all larval stages except for Stage I zoeae of *Sclerocrangon zenkevitchi* and *S. boreas*, which lack a rostrum, and Stage I zoeae of *Paracrangon echinata*, which have a spinulose rostrum (Birshteyn[4] and Vinogradov 1953; Kurata 1964b; Makarov 1968).

Spines on the Carapace

The presence or absence of certain spines on the carapace is useful for distinguishing between families and identifying one or more stages. The larval carapace (Fig. 1A, C) may have supraorbital spines (so), pterygostomian spines (pt), antennal spines (as), and anteroventral denticles (ad). Supraorbital spines are absent in all larval stages of the Crangonidae. For pandalid and hippolytid larvae, supraorbital spines are usually absent in Stage I and the megalopa, but present in the intermediate zoeal stages. However, there are some exceptions to these generalizations. Larvae of *Pandalus hypsinotus* have supraorbital spines only in Stages II and III, and larvae of *P. kessleri* have supraorbital spines only in Stage II (Kurata 1955; Haynes 1976). Larvae of *P. prensor* are without supraorbital spines in all larval stages (Mikulich and Ivanov 1983). In the Hippolytidae, *Spirontocaris spinus*, *S. lilljeborgii*, and probably *S. phippsii* have supraorbital spines in all larval stages (the spines are minute in Stage I). *Spirontocaris ochotensis* has minute supraorbital spines in Stage I; whether supraorbital spines develop later is unknown. *Lebbeus groenlandicus*, a species with abbreviated development, has supraorbital spines only in Stage II and the megalopa (Stage III) Pike and Williamson 1961; Haynes 1978b, 1981). In all three families, pterygostomian spines are usually present in all larval stages. Antennal spines are often absent in Stage I but usually develop in later stages. Anteroventral denticles are most prevalent in the early stages and usually, but not always, disappear during larval development. Branchiostegal and hepatic spines are rarely, if ever, present in the larval stages.

Eyes

Development of the eyes is the same for nearly all members of the three families. The eyes are compound and sessile in Stage I and are stalked in later stages. The exception, Stage I *Pandalopsis coccinata*, has compound eyes that are only partially attached to the carapace (Kurata 1964a).

Antennules

In the Pandalidae and nearly all hippolytid and

[4]Translator's spelling of "Birstein".

crangonid larvae, the peduncle of the antennule (Fig. 1B, ap) is unsegmented in Stage I and becomes three segmented later, usually in Stage II. The exceptions are Stage I *Sclerocrangon boreas*, which has a 3-segmented antennule; Stage II *Eualus suckleyi* and *E. fabricii*, which have 2-segmented peduncles; and both Stages I and II *Lebbeus polaris* and *L. groenlandicus*, which have unsegmented peduncles.

In Stage I pandalid and hippolytid larvae, the inner flagellum (Fig. 1B, if) of the antennule is usually a plumose seta, whereas in Stage I crangonid larvae, it is usually a setose spine. The only described exceptions are Stage I larvae of *Pandalus prensor*, *Sclerocrangon boreas*, *S. salebrosa*, and *S. zenkevitchi*. In Stage I *Pandalus prensor*, the inner flagellum is spine shaped and has a few simple setae medially. In Stage I *S. boreas*, *S. salebrosa*, and *S. zenkevitchi*, the inner flagellum is an oblong projection that is naked except for a few minute, simple setae terminally (Birshteyn and Vinogradov 1953; Makarov 1968; Haynes 1978b, 1981; Mikulich and Ivanov 1983).

Antennae

Segmentation of the tip of the antennal scale (Fig. 1C, sc, ss) is an important characteristic for distinguishing crangonid larvae from pandalid and hippolytid larvae. In crangolid larvae, the scale tip is unsegmented in all stages. In pandalid and hippolytid larvae, the scale tip is unsegmented in only four species: *Pandalopsis coccinata*, *Pandalus kessleri*, *P. prensor*, and possibly *Heptacarpus* (= *Spirontocaris*) *tridens* (Needler 1934; Kurata 1955, 1964a, b; Mikulich and Ivanov 1983). The absence of segmentation of the scale tip of *Pandalopsis coccinata*, *Pandalus kessleri*, and *P. prensor* is related to the extremely precocious development of these species. *Heptacarpus tridens*, however, has unabbreviated development (Needler 1934) and, presumably, a segmented tip. Needler (1934) may not have observed segmentation of the scale in *H. tridens* because she based her description on unstained larvae (staining emphasizes segmentation (Haynes 1976)).

Mandibles

Mandibles (Fig. 1D) are described for most pandalid larvae, but descriptions of mandibles for hippolytid and crangonid larvae in the northern North Pacific Ocean are usually limited to Stage I. I have supplemented these limited descriptions with information on larvae from other areas, particularly the North Sea. Descriptions of late stage larvae from the northern North Pacific Ocean are needed, however, to verify development of mandibles in hippolytid and crangonid larvae.

Zoeae of Pandalidae, Hippolytidae, and Crangonidae have similar mandibles in all stages, and both molar and incisor processes are present. In Stage I, the incisor processes of the left and right mandibles are typically biserrate or triserrate. The number of teeth increases in later stages. In some species, the left mandible also has a subterminal tooth and a lacinia mobilis (movable spine adjacent to incisor process; Fig. 1E). The subterminal tooth and lacinia mobilis are usually, if not always, absent on the right mandible. In the Crangonidae, the incisor process eventually becomes a molar process, usually at the megalopa.

The most distinctive character of the mandible is the absence of a palp in the zoeal stages. This palp first appears in the megalopa or first juvenile stage of Pandalidae and in the megalopa or later stages of the Hippolytidae. In one exception, *Pandalopsis coccinata*, the palp is present and segmented as early as Stage I (Kurata 1964a). The palp is absent in all stages of Crangonidae, including the adults.

The mandibular palp of the Hippolytidae may develop somewhat later than the mandibular palp of the Pandalidae. For instance, in some species of Hippolytidae, the palp may not appear until as late as the third or fourth juvenile stage (Lebour 1936), and in some genera, such as *Hippolyte*, the absence of the palp in the adult may mean the palp is absent in the larvae also. The palp eventually becomes three segmented in the Pandalidae and two segmented in the Hippolytidae.

Maxillules

Lebour (1930) stated that *Pandalus* larvae have no subterminal seta (Fig. 1F, st) on the basipodite of the maxillule (Fig. 1F, Mx_1, b). Yet, the seta is present in some or all larval stages of *Pandalus kessleri*, *P. tridens*, *P. stenolepis*, *P. borealis*, *P. goniurus*, *P. jordani*, *P. hypsinotus*, and *Pandalopsis coccinata*. The seta is also present in the early stages of *Pandalus montagui*, *P. propinquus*, *Pandalina brevirostris*, and *Dichelopandalus bonnieri* that were collected from waters off Great Britain (Needler 1938; Kurata 1955, 1964a; Pike and Williamson 1964; Modin and Cox 1967; Lee 1969; Haynes 1976, 1978a, 1979, 1980a). The subterminal seta is absent in hippolytid and crangonid larvae described from the North Pacific Ocean but is present in larvae of *Hippolyte inermis* and *H. varians* from waters off Great Britain (Lebour 1931). According to Gurney (1942) and Pike

and Williamson (1964), the seta is probably the vestige of an exopodite; however, Williamson (1982) regards it as a vestigial epipodite or pseudoepipodite.

Maxillae

Development of the scaphognathite (exopodite) of the maxilla (Fig. 1G) is related to development of the larvae. Most species that lack precocious development have a scaphognathite that is not lobed proximally and has only a few (usually ≤ 12) plumose setae only on its outer margin. The scaphognathite gradually becomes lobed proximally in subsequent stages, and the outer margin becomes fringed with many plumose setae. In species with precocious development, the scaphognathite is lobed proximally and fringed with many plumose setae in Stage I.

The number of plumose setae is sometimes used for distinguishing Stages I or II of similar species. For instance, Stage I zoeae of *Pandalus borealis* and *P. goniurus* are similar morphologically, and in these species the scaphognathite has 12 and 5 plumose setae, respectively. In later stages, however, the number of plumose setae fringing the scaphognathite becomes too great to be practical for distinguishing zoeae of similar species.

Maxillipeds

The number of natatory setae on the exopodite of each maxilliped (Fig. 1H-J) is helpful for distinguishing Stage I hippolytid and crangonid zoeae from Stage I pandalid zoeae. All Stage I hippolytid and most Stage I crangonid zoeae have 4, 5, 5 natatory setae on the exopodites of maxillipeds 1-3. In the Pandalidae, all Stage I pandalid zoeae, except *Pandalus stenolepis*, have ≥ 8 natatory setae on the exopodites of at least two pairs of maxillipeds. Stage I *P. stenolepis*, however, cannot be differentiated from Stage I hippolytid and crangonid zoeae based only on natatory setae because Stage I *P. stenolepis* also has 4, 5, 5 natatory setae on the exopodite of each maxilliped.

The absence or reduction in numbers or size of natatory setae on the exopodites of maxillipeds is associated with markedly precocious development. This is especially true for *Pandalopsis coccinata*, *Sclerocrangon boreas*, and *S. zenkevitchi*. Each of these species has only one zoeal stage before molting to the megalopa. In *P. coccinata*, the natatory setae are absent from the third maxilliped. In *S. boreas*, the number of natatory setae on maxillipeds 1-3 is 2, 3, 4, respectively; and the setae are reduced in size. *Sclerocrangon zenkevitchi* zoeae do not have natatory setae on the maxillipeds.

Apparently, the absence or reduction in size of natatory setae prevents zoeae from being planktonic. Zoeae of *S. boreas* and *S. zenkevitchi* (collected at sea) cling to the pleopods of the adult (Birshteyn and Vinogradov 1953; Makarov 1968). Zoeae of *P. coccinata* are rarely, if ever, taken in plankton tows (Kurata 1964a).

Pereopods

The presence of exopodites (Fig. 1J, ex) on certain pereopodal pairs is an important morphological character for identifying shrimp larvae. Exopodites are present on pereopods 1, 1 and 2, 1-3, or 1-4, depending on genus or species (Fig. 1K-M).

Species with unabbreviated development usually develop an exopodite on each pereopod. In most species with ≥ 5 zoeal stages, the exopodites are characteristically small, naked, and nonfunctional at Stage I but functional (have natatory setae) at Stage II or III. Development of exopodites on pereopods tends to be suppressed in species with < 5 zoeal stages.

In the Pandalidae, species that have segmented pereopods directed vertically under cephalothorax (i.e., developed pereopods) in Stage I—*Pandalopsis coccinata*, *Pandalopsis dispar*, *Pandalus kessleri*, *Pandalus danae*, *Pandalus hypsinotus*, and *Pandalus prensor*—also have exopodites or vestigial exopodites on pereopods 1 and 2. Species that have unsegmented pereopods directed anteriorly under cephalothorax (i.e., undeveloped pereopods) in Stage I—*Pandalus tridens*, *P. stenolepis*, *P. borealis*, *P. goniurus*, and *P. jordani*—also have exopodites on pereopods 1-3 (the exopodites are undeveloped in Stage I and develop in later stages). An exception is *P. platyceros*, which in Stage I has developed pereopods and exopodites on pereopods 1-3 (Haynes 1980b).

Of the Hippolytidae, only larvae of the genus *Lebbeus* have developed pereopods in Stage I. *Lebbeus polaris* has vestigial exopodites on pereopods 1 and 2 in Stage I and on pereopod 1 in Stage II. *Lebbeus groenlandicus* has vestigial exopodites on pereopods 1 and 2 in Stage I and no exopodites on pereopods in Stages II or III (Haynes 1978b, 1981).

In the Crangonidae, most species with developed pereopods in Stage I (*Argis crassa*, *A. lar*, *A. dentata*, *Sclerocrangon boreas*, and *S. salebrosa*) are either without exopodites or have rudimentary exopodites. An exception is *S. zenkevitchi*, which has an exopodite on pereopod 1 in Stage I (Birshteyn and Vinogradov 1953).

Which pereopods have exopodites can differ for different species of a genus. For example, the genus *Pandalus* includes larvae that have exopodites on pereopods 1 and 2 or 1-3 (Haynes 1980a). The genus *Eualus* includes larvae that have exopodites on pereopods 1-3 or 1-4 (Haynes 1981). Larvae of *Crangon* typically have an exopodite only on pereopod 1; however, larvae of *C. franciscorum angustimana* have exopodites on pereopods 1 and 2 (Haynes 1980b).

Abdomen

The presence or absence of posterolateral spines (Fig. 1A, pl) on the abdomen is often an important character for identifying the families of caridean larvae. Specimens of pandalid larvae from the northern North Pacific Ocean do not have posterolateral spines. Crangonid larvae, however, usually have posterolateral spines on somite 5, except for larvae of *Sclerocrangon boreas* and *S. zenkevitchi* (Birshteyn and Vinogradov 1953; Makarov 1968). Larvae of Hippolytidae also have posterolateral spines. Posterolateral spines are present on somites 4 and 5 in *Lebbeus* larvae and on somite 5 in *Hippolyte* larvae, but are absent in *Heptacarpus* larvae.

The number of abdominal somites with posterolateral spines is not always the same for all species of a genus. For instance, *Spirontocaris* larvae and most *Eualus* larvae have posterolateral spines on somites 4 and 5, or 5. In some species of *Eualus*, the posterolateral spines may be absent.

Most pandalid and hippolytid larvae lack dorsal spines or teeth on the abdomen. The only known exception is *Spirontocaris spinus*, which has a distinct dorsal tooth on the posterior margin of abdominal somite 3 in the megalopa (Stage VI) (Pike and Williamson 1961).[5]

Of the described crangonid larvae of the northern North Pacific Ocean, only *Crangon septemspinosa*, *C. affinis*, *C. alaskensis*, and *C. franciscorum angustimana* have a dorsal spine (Fig. 1A, ds) on somite 3 (Makarov 1967; Loveland 1968; Haynes 1980b). *Paracrangon echinata* has dorsal spines on somites 1-5 (Kurata 1964b).

Some zoeae have spinules on the posterior margins of abdominal somites. These spinules are present in zoeae of *Pandalus platyceros*, *P. tridens*, *P. stenolepis*, *Eualus suckleyi*, *E. fabricii*, *Argis crassa*, *A. dentata*, and *Crangon communis*. The number and size of spinules decrease in later stages.

[5]This spine is present in all subsequent stages (juvenile and adult) and should probably not be regarded as a larval character.

Telson

The shape of the telson is useful in determining the stage of development of caridean larvae. For most Stage I-III pandalid and hippolytid larvae, the posterior margin of the telson is about twice the width of the anterior margin. At about Stage IV, the shape of the telson narrows posteriorly, and from Stage IV on, the posterior margin of the telson is noticeably less than twice the anterior width. Eventually, the telson narrows posteriorly, as in the adult. Although the telson remains triangular in all stages of crangonid larvae, it is somewhat narrower in the megalopa or first juvenile stage than in earlier stages.

For caridean larvae with unabbreviated development, the typical number of telsonic setae (Fig. 1O, ts) is 7 + 7 in Stage I and 8 + 8 in later stages. These numbers of telsonic setae are seldom exceeded in later stages and are often reduced by either loss or transformation of certain pairs (usually pairs of 2 or 3) into small setae or hairs.

A larger number of telsonic spines are more commonly associated with abbreviated development than with unabbreviated development (Gurney 1942; Pike and Williamson 1964), and this is generally true for caridean larvae of the North Pacific Ocean. For example, *Pandalus kessleri*, a species with four larval stages, has 16 + 16 telsonic setae in Stage I, and *Pandalopsis coccinata*, a species with three (or two) larval stages, has 28 + 28 telsonic setae in Stage I (Haynes 1980a). Examples can also be found in the other families of Caridea. In the Crangonidae, *Sabinea septemcarinata* has 16 + 16 telsonic setae in Stage I and three larval stages, whereas *Sclerocrangon salebrosa* has 22 + 22 telsonic setae in Stage I and one larval stage (Williamson 1960; Makarov 1968). In the Hippolytidae, *Lebbeus polaris* has 9 + 9 telsonic setae in Stage I and four larval stages; *L. groenlandicus* has a total of 21 telsonic setae in Stage I and three larval stages (Haynes 1978b, 1981).

All larvae of Hippolytidae except larvae of the genus *Hippolyte* have an anal spine (Fig. 1O, al). For *Hippolyte* larvae, the anal spine is absent in all described stages. When pandalid and crangonid larvae have unabbreviated development, the anal spine usually appears at about Stage II in pandalid larvae and about Stage IV in crangonid larvae.

However, the presence of an anal spine has little value in the identification of pandalid and crangonid larvae with abbreviated development. In pandalid larvae with abbreviated development, the anal spine first appears at different stages in different species.

For example, the spine is present in Stage I *Pandalus kessleri*, but absent in *P. hypsinotus* until Stage III. The stage at which the anal spine first appears in crangonid larvae with abbreviated development has not been reported.

KEY TO STAGE OF DEVELOPMENT

Larvae of most of the species in this report can be keyed to stage based on development of the eyes and tail fan (Key I; Table 1). Key I is mostly applicable to species whose larval development is not markedly abbreviated (i.e., those with ≥ 5 zoeal stages). In species with unabbreviated development, exopodites on pereopods are characteristically undeveloped in Stage I and usually have natatory setae beginning at Stage II or III. Most of the species excluded from the key (Table 2) have ≤ 4 zoeal stages, and exopodites on pereopods are either absent in all stages, vestigial in Stages I and II, or have natatory setae as early as Stage I. Key I is limited because it does not differentiate between the latest stages and uses only one or two characters, which may be absent in damaged specimens.

For pandalid shrimp, Key I can be supplemented by keys to stages for each species (i.e., Keys IV and VI-XI, which have characters not given in Key I and distinguish between the latest stages). With a few

TABLE 1.—Species included in keys.

Pandalidae Haworth 1825	Hippolytidae Bate 1888	Crangonidae White 1947
Pandalopsis Bate 1888	*Eualus* Thallwitz 1892	*Argis* Krøyer 1842
P. coccinata Urita 1941	*E. barbatus* (Rathbun 1899)	*A. crassa* (Rathbun 1899)
P. dispar Rathbun 1902	*E. fabricii* (Krøyer 1841)	*A. dentata* (Rathbun 1902)
Pandalus Leach 1814	*E. gaimardii* (H. Milne Edwards 1837)	*A. lar* (Owen 1839)
P. borealis Krøyer 1838	*E. herdmani* (Walker 1898)	*Crangon* Fabricius 1798
P. danae Stimpson 1857	*E. macilentus* (Krøyer 1841)	*C. affinis* de Haan 1849
P. goniurus Stimpson 1860	*E. pusiolus* (Krøyer 1841)	*C. alaskensis* Lockington 1877
P. hypsinotus Brandt 1851	*E. suckleyi* (Stimpson 1864)	*C. communis* Rathbun 1899
P. jordani Rathbun 1902	*Heptacarpus* Holmes 1900	*C. dalli* Rathbun 1902
P. kessleri Czerniavski 1878	*H. brevirostris* (Dana 1852)	*C. franciscorum angustimana* Rathbun 1902
P. platyceros Brandt 1851	*H. camtschaticus* (Stimpson 1860)	*C. septemspinosa* Say 1818
P. prensor Stimpson 1860	*H. paludicola* (Holmes 1900)	*Mesocrangon* Zarenkov 1965
P. stenolepis Rathbun 1902	*H. tridens* (Rathbun 1902)	*M. intermedia* (Stimpson 1860)
P. tridens Rathbun 1902	*Hippolyte* Leach 1815	*Paracrangon* Dana 1852
	H. clarki Chace 1951	*P. echinata* Dana 1852
	Lebbeus White 1847	*Sabinea* J. C. Ross 1835
	L. groenlandicus (Fabricius 1775)	*S. septemcarinata* (Sabine 1824)
	L. polaris (Sabine 1821)	*Sclerocrangon* G. O. Sars 1883
	Spirontocaris Bate 1888	*S. boreas* (Phipps 1774)
	S. arcuata Rathbun 1902	*S. salebrosa* (Owen 1839)
	S. lilljeborgii (Danielssen 1859)	*S. zenkevitchi* Birstein and Vinogradov 1953
	S. murdochi Rathbun 1902	
	S. ochotensis (Brandt 1851)	
	S. phippsii (Krøyer 1841)	
	S. spinus (Sowerby 1805)	
	S. spinus var. *intermedia* Makarov 1941	

TABLE 2.—Species that cannot be keyed to stage of development using Key I.

Pandalidae	Hippolytidae	Crangonidae
Pandalopsis	*Lebbeus*	*Argis*
P. coccinata	*L. groenlandicus*	*A. crassa*
P. dispar	*L. polaris*	*A. dentata*
Pandalus		*A. lar*
P. danae (Stage III)		*Sclerocrangon*
P. hypsinotus (Stage III)		*S. boreas*
P. kessleri		*S. salebrosa*
P. platyceros		*S. zenkevitchi*
P. prensor		*Sabinea*
P. stenolepis (Stage III)		*S. septemcarinata*

exceptions, Key I can be used to identify larval stages of *Pandalus hypsinotus*, *P. danae*, and *P. stenolepis*. The exceptions are in Stage III *P. hypsinotus*, the endopodite of the uropods is setose and nearly the same length as the exopodite, and in Stage III *P. danae* and *P. stenolepis*, the endopodite is setose and somewhat shorter than the exopodite.

Key I.—Generalized key to stages of most species of pandalid, hippolytid, and crangonid larvae described from waters of the northern North Pacific Ocean. (This key cannot be used for all species, see Table 2 for exceptions.)

1. Uropods absent 2
   Uropods present 3

2. Eyes sessile; telson with 7 + 7 setae . . . . Stage I
   Eyes stalked; telson with 8 + 8 setae . . Stage II

3. Posterior width of telson about twice its anterior width. Endopodite of uropod (Fig. 1O, en) with relatively few setae and noticeably shorter than exopodite (Fig. 1O, ex) . . . . . Stage III
   Posterior width of telson noticeably less than twice its anterior width. Endopodite of uropod setose and about as long as exopodite . . . . . Stage IV and later

LARVAL CHARACTERS OF FAMILIES

Crangonid larvae are relatively easy to distinguish from pandalid or hippolytid larvae; however, pandalid and hippolytid larvae often are difficult to distinguish from each other, especially in the early stages. Briefly, the characteristics of crangonid larvae are 1) the tip of the antennal scale is always unsegmented, 2) the inner flagellum of the antennule is a setose spine or oblong projection, 3) an exopodite is usually only on pereopod 1 and never on pereopods 3-5, and 4) in later stages, pereopod 1 is subchelate, and the telson widens posteriorly. No known pandalid or hippolytid larvae possess this combination of characters.

The following set of characters, although not without exceptions, is probably the most useful set for distinguishing between pandalid and hippolytid larvae of the northern North Pacific Ocean. Pandalid larvae 1) always have a long rostrum (greater than 1/4 carapace length) that has teeth from Stage III on, 2) the basipodite of the maxillule has a subterminal seta, 3) exopodites are only on pereopods 1-2 or 1-3, 4) the abdomen lacks posterolateral spines, and 5) an anal spine is absent in Stage I. On the other hand, hippolytid larvae 1) have a rostrum that is long and without teeth (especially from Stage III on), 2) in all stages, the basipodite of the maxillule lacks a subterminal seta, 3) exopodites are on pereopods 1-2, 1-3, or 1-4 (rather than only on pereopods 1-2 or 1-3), 4) the abdomen has posterolateral spines, and 5) an anal spine is present in Stage I (except larvae of the genus *Hippolyte*).

Late-stage (Stage IV and later) pandalid and hippolytid larvae can often be distinguished from each other by shape of eyes and distance between bases of antennules. The eyes of pandalid larvae taper toward the base, and the distance between bases of antennules is more than the width of an antennule. The eyes of hippolytid larvae are almost cylindrical, and the distance between antennules is less than the width of an antennule. In Stages I-III, distinctions in the shape of eyes and distance between bases of antennules are usually not useful.

Shape of the larva is often helpful in distinguishing between pandalid and hippolytid larvae during the initial sorting. Pandalid larvae, when viewed laterally, have nearly straight antennules, whereas the antennules of many hippolytid larvae curve upward. The abdomen of pandalid larvae appears slightly longer than the abdomen of hippolytid larvae in relation to length of the larva as a whole. These two characters are difficult to quantify and are best learned through examination of specimens of known identity. Additional morphological characters that distinguish larvae of the Pandalidae, Hippolytidae, and Crangonidae are given in the synopsis of each family.

PANDALIDAE

(Genera *Pandalopsis* and *Pandalus*)

In all stages, rostrum long, styliform, or slightly sinuate; plumose seta on inner flagellum of antennule (Fig. 1B, A_1, if); maxillule with or without subterminal seta (Fig. 1F, Mx_1, st) on basipodite; abdomen without dorsal spines, keels, or posterolateral spines; pereopod 1 never subchelate. In Stage I, supraorbital spine absent; rostrum with teeth in some species; anal spine absent in some species. In early stages of most species, antennal scale segmented at tip. In Stages I and II of some species with abbreviated development, vestigial exopodites on pereopods 1 and 2 or 1-3. In later stages, developed exopodites on pereopods 1 and 2 or 1-3, never on 1-4; setose setae on endopodite of each pleopod (Stage V

TABLE 3.—Principal morphological characteristics and number of larval stages of known larvae of pandalid shrimp of the northern North Pacific Ocean. + = yes; − = no.

Species	Pereopods bearing an exopodite	Pereopods poorly developed in Stage I	Spinules on abdominal somites	Denticles on carapace margin	No. of telson spines in Stage I	No. of larval stages
Pandalopsis coccinata	1-2	—	—	—	28 + 28	3
P. dispar	1-2	—	—	—	12 + 12	7
Pandalus kessleri	1-2	—	—	—	16 + 16	4
P. danae	1-2	—	—	—	7 + 7	6
P. hypsinotus	1-2	—	—	—	7 + 7	7
P. platyceros	1-3	—	+	+	8 + 8	5
P. prensor	1-2	—	—	—	9 + 9	5
P. tridens	1-3	+	+	+	7 + 7	8
P. stenolepis	1-3	+	+	+	7 + 7	6
P. borealis	1-3	+	—	—	7 + 7	6
P. goniurus	1-3	+	—	—	7 + 7	6
P. jordani	1-3	+	—	—	7 + 7	13

on); telson does not widen posteriorly, has > 1 pair of lateral spines (Stage IV on).

The principal morphological characters and number of larval stages of known larvae of pandalid shrimp of the northern North Pacific Ocean are summarized (Table 3, modified from Haynes 1980b).

Genus *Pandalopsis* Bate

Larval development abbreviated; larvae relatively large (≥ 10.0 mm in Stage I). In all described stages, rostrum with teeth; carapace without denticles; antennal flagellum as long as or longer than body; thoracic appendages noticeably long and thin; abdominal somites without spines or spinules, somites not flared laterally. In Stage I, pereopods segmented; telson with at least 12 + 12 setae; telson jointed with abdominal somite 6.

Pandalopsis coccinata Urita

Only Stage I described, known parentage; figure 7 in Kurata (1964a).

Eyes partially fused with carapace; antennal flagellum same length as body; mandibular palp with 3 segments; seta on basipodite of maxillule; rudimental exopodite on maxilliped 3 and pereopods 1 and 2; telson discoid with 55 or 56 setae (Fig. 3). Length: Stage I, 15.5 mm. Range: Japan (Kurata 1964a), no depth given.

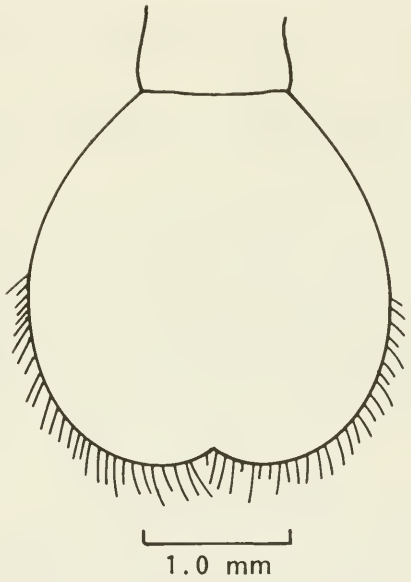

FIGURE 3.—Telson, Stage I zoea of *Pandalopsis coccinata*.

Pandalopsis dispar Rathbun

Possibly 7 larval stages.

Stage I, known parentage; Stages II, III, and V?, from plankton; figures 11-13 in Berkeley (1930).

In all stages, basipodite of maxillule without subterminal seta. In Stage I, eyes sessile; antennal flagellum about 1/4 longer than body. Telson fan shaped in early stages. Until at least Stage V, mandibles without palps; developed exopodites on maxilliped 3 and pereopods 1-2. Length: Stage I, 10.0 mm. Range: Pribilof Islands, Bering Sea to Manhattan Beach, OR; depth, 46-649 m (Butler 1980).

Key II.—Larval stages of *Pandalopsis dispar*.

1. Rostrum curves dorsally (Fig. 4); exopodites on pereopods without natatory setae . . . Stage I

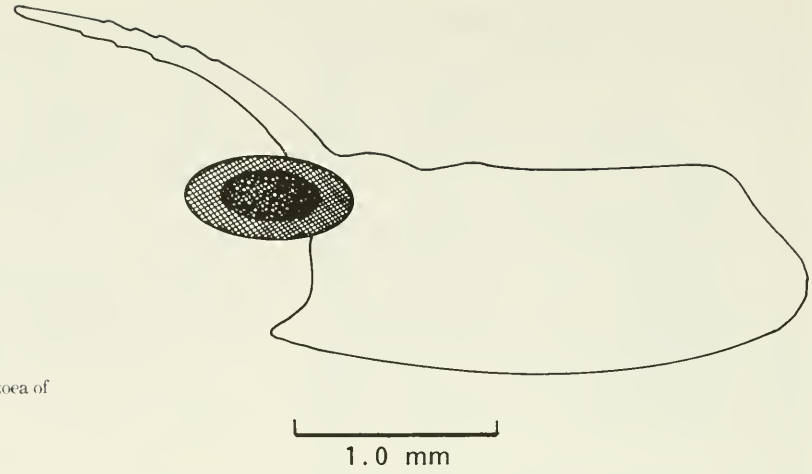

FIGURE 4.—Carapace, Stage I zoea of *Pandalopsis dispar*.

Rostrum horizontal; exopodites on pereopods with natatory setae 2

2. Uropods absent; length of larvae ≤ 13.0 mm . . . . . Stage II
Uropods present; length of larvae > 13.0 mm 3

3. Endopodite of uropod noticeably shorter than exopodite; length of larvae ≅ 16.0 mm . . . . . Stage III
Endopodite and exopodite of uropod same length; length of larvae > 16.0 mm . . . . . Stage IV and later[6]

Genus *Pandalus* Leach

Most species with unabbreviated development. In all stages, thoracic appendages not especially long or thin. In Stage I, larvae usually 5-6 mm long; rostrum usually without teeth; pereopods usually undeveloped and tucked under cephalothorax; telson with 7 + 7 setae; telson not jointed with abdominal somite 6. In early stages of some species, anteroventral margin of carapace with denticles; posterior margin of abdominal somites with spinules.

Pandalus borealis Krøyer[7]

Six larval stages.

Stages I-V, VI (megalopa), and VII and VIII (juveniles); all stages from both known parentage and plankton; figures 1-7 in Haynes (1979).

Stage I, known parentage; Stages II-VII from plankton; figures 1-3 in Kurata (1964a).

Stage I, known parentage; Stages II-VI from plankton; figures 7 and 8 in Berkeley (1930).

Stages I-V from plankton; described as "*P. propinquus* (?)" by Stephensen (1912); figures 22-31 in Stephensen (1912).

Stage III from plankton; described as "*Spirontocaris* larva Nr. 4" by Stephensen (1916); figure 11 in Stephensen (1916). Also described as *P. propinquus*, Stage VI? by Stephensen (1916); figure 17 (chelae only) in Stephensen (1916).

Stage IV from plankton; described as "*Dymas typus*" (?) by Krøyer (1861, as cited in Stephensen 1935). No figures.

"Post larval" from plankton; Plate VII in Sars (1900). Probably megalopa of *P. borealis* (see Haynes 1979).

Not Stages I-VIII *P. borealis* as described by Sars (1900) and figured in Plates I-VI. Correct identity, *Caridion gordoni* (see Berkeley 1930; Lebour 1930).

In all described stages, carapace and abdominal somites not flared laterally; basipodite of maxillule

[6]A later larval stage, probably Stage V or VI, characterized by rostrum with 25 dorsal spines: 1 spine near tip, 14 dorsal spines, 10 ventral spines. Chela of pereopod 2 (Fig. 1, P_2, ch) developed, and carpopodite (Fig. 1, ca) with a few faint segments; abdominal somites and pleopods essentially adult; telson narrows posteriorly and has 7 + 7 slightly plumose, terminal setae and 6 pairs of single lateral spines. Length: 30.0 mm (Berkeley 1930).

[7]Larvae of *Pandalus borealis* and *Pandalus goniurus* are often found together in plankton. They are especially similar in the early stages and are difficult to distinguish. For identification of these two species, I have included Table 4, which lists by larval stage the most readily observable differences for both species. In general, larvae of *P. goniurus* are smaller than those of *P. borealis*. In Stages I-III, *P. goniurus* larvae have fewer setae on the antennal scale and certain mouth parts than *P. borealis* larvae. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, pereopod 2 is more developed, and the pleopods are fringed with more setae than larvae of *P. goniurus* (Haynes 1979).

with subterminal seta. Carapace usually with denticles on anteroventral margins in Stages I-V. Rostrum without teeth until Stage III; rostral tip bifid in Stage V. In Stage I, exopodites of maxillipeds 1, 2, and 3 with 5 or 6, 13 or 14, and 16 natatory setae, respectively; pereopods tucked under carapace; left mandible with a lacinia mobilis; basipodite of maxillule with 9 spinulose spines terminally; scaphognathite of maxilla with 12 setae along outer margin. Length: Stages I-VI, 6.5-20.2 mm. Range: Sea of Japan to Chukchi Sea to Columbia River mouth (northwestern United States); Barents Sea to North Sea; western Greenland to Gulf of Maine; depth, 16-1,380 m (Butler 1980).

Key III.—Larval and first juvenile stages of *Pandalus borealis* (see footnote 7 and Table 4).

1. Eyes sessile; pleopods absent; telson with 7 + 7 setae ..... Stage I
   Eyes stalked; pleopods present as minute buds; telson with 8 + 8 setae 2

2. Rostrum without teeth; pereopods 4 and 5 tucked under cephalothorax; uropods enclosed ..... Stage II
   Rostrum with ≥ 1 dorsal tooth at base; pereopods 4 and 5 extend ventrally; uropods free ... 3

3. Rostrum with 1 or 2 dorsal teeth at base; antennal flagellum with 8 segments and same length as scale; endopodite of uropod about 1/3 length of exopodite ..... Stage III
   Rostrum with ≥ 4 dorsal teeth; antennal flagellum with ≥ 15 segments and longer than scale; endopodite of uropod > 1/2 length of exopodite 4

4. Rostrum with 4-8 dorsal teeth (usually 6), without ventral teeth; tip of rostrum styliform; pleopods with a few small setae at tip; endopodite of uropod about 2/3 length of exopodite ..... Stage IV
   Rostrum with > 8 dorsal teeth and ≥ 4 ventral teeth; tip of rostrum bifid; pleopods setose; endopodite of uropod nearly as long as expodite 5

5. Rostrum with 9-12 dorsal teeth and 4 or 5 small ventral teeth; carapace with supraorbital spine; telson with 2 spines on each lateral margin; lateral margins of telson nearly parallel ..... Stage V
   Rostrum with > 12 dorsal teeth and ≥ 6 distinct ventral teeth; carapace without supraorbital spine; telson with ≥ 4 spines on each lateral margin; lateral margins of telson taper posteriorly 6

6. Mandibles without palps; exopodites on maxillipeds and pereopods reduced in size; lateral margins of telson converge posteriorly but widen slightly at junction with posterior margin ..... Stage VI (megalopa)
   Mandibles with palps; vestigial exopodites on maxillipeds and pereopods; telson with lateral margins converging to narrow tip, as in adult ..... Stage VII (first juvenile)

Pandalus danae Stimpson

Six larval stages.
Stage I, known parentage; Stages II-VI, from plankton; figures 3-5 in Berkeley (1930).

In all described stages, carapace without denticles on anteroventral margin; basipodite of maxillule without subterminal seta; posterior margins of abdominal somites without spinules. In Stage I, thoracic appendages developed; naked exopodites on pereopods 1 and 2; telson jointed with abdominal somite 6. Length: Stages I-VI, 5.7-17.0 mm. Range: Resurrection Bay, AK, to Point Loma, CA; depth, intertidal to 185 m (Butler 1980).

Key IV.—Larval stages of *Pandalus danae*.

1. Eyes sessile; carapace without supraorbital spine; exopodites on pereopods 1 and 2 without natatory setae ..... Stage I
   Eyes stalked; carapace with supraorbital spines; exopodites on pereopods 1 and 2 with natatory setae 2

2. Rostrum without teeth; uropods enclosed ... . Stage II
   Rostrum with teeth; uropods free 3

3. Rostrum with 2 or 3 minute dorsal teeth at base; endopodite of uropods noticeably shorter than exopodite ..... Stage III
   Rostrum with ≥ 8 teeth dorsally; endopodite of uropods same length as exopodite 4

4. Pleopods small, slightly cleft buds; telson widens slightly posteriorly ..... Stage IV

TABLE 4.—Morphological characteristics for distinguishing between larvae of *Pandalus borealis* and *P. goniurus* reared in situ in Kachemak Bay, Alaska (from Haynes 1979).

Stage and characteristic	*Pandalus borealis*	*Pandalus goniurus*
Stage I zoea:		
Mean total length	6.7 mm (range 6.5-7.3 mm; 25 specimens)	4.0 mm (range 3.7-4.2 mm; 10 specimens)
Number of plumose setae fringing antennal scale	19	9
Number of spines terminally on basipodite of maxillule	9	5
Number of plumose setae on scaphognathite (in addition to single proximal seta)	11	4
Number of natatory setae on each exopodite:		
maxilliped 1	5-6	4
maxilliped 2	13-14	8
maxilliped 3	16	12
Stage II zoea:		
Mean total length	7.5 mm (range 6.7-8.2 mm; 25 specimens)	5.9 mm (range 4.5-5.3 mm; 10 specimens)
Number of plumose setae fringing antennal scale	about 25	about 19
Number of natatory setae on each exopodite:		
maxilliped 1	7	6
maxilliped 2	16	12
maxilliped 3	18	14
pereopods 1, 2, 3	16, 16, 12	12, 8, 8
Stage III zoea:		
Mean total length	9.5 mm (range 9.0-10.0 mm; 10 specimens)	6.2 mm (range 6.0-6.6 mm; 10 specimens)
Rostrum	1-2 conspicuous teeth	1 inconspicuous tooth
Antennal flagellum	8-segmented	3-segmented
Antennal scale	about 30 setae	about 20 setae
Stage IV zoea:		
Mean total length	13.0 mm (range 12.6-13.2 mm; 10 specimens)	7.7 mm (range 6.8-8.3 mm; 10 specimens)
Rostrum	6-7 dorsal teeth	2 dorsal teeth
Antennal flagellum	about 1½ times length of scale, extending past tips of plumose setae	longer than scale but not extending past tips of plumose setae
Propodite of pereopod 2	projected anteriorly about 1/2 length of dactylopodite	projected anteriorly only slightly
Pleopods	segmented, pleopod 2 about 1/2 height of abdominal somite	unsegmented, pleopod 2 about 1/3 height of abdominal somite
Stage V zoea:		
Mean total length	16.0 mm (range 15.2-17.1 mm; 10 specimens)	10.3 mm (range 8.2-11.3 mm; 10 specimens)
Rostrum	9-12 dorsal teeth; tip bifid; 45 partially developed ventral teeth	5-6 dorsal teeth; tip not bifid (but may show slight protuberance); no ventral teeth
Chela of pereopod 2	fully formed	not fully formed, propodite extension about 1/2 length of dactylopodite
Pleopods	with appendix interna; fringed with plumose setae; 2 as long or longer than height of abdominal somite	without appendix interna; 2-4 simple setae terminally; pleopod 2 about 2/3 height of abdominal somite
Stage VI (megalopa):		
Mean total length	18.5 mm (range 17.4-20.2 mm; 5 specimens)	13.8 mm (range 11.1-15.8 mm; 6 specimens)
Rostrum	13-15 dorsal teeth, 6-7 ventral teeth	8-9 dorsal teeth, 4-5 ventral teeth

Pleopods distinct and biramous; sides of telson parallel or narrow posteriorly 5

5. Carapace with supraorbital spine; exopodites on maxillipeds and pereopods have natatory setae . . . . . Stage V
Carapace without supraorbital spine; exopodites on maxillipeds and pereopods naked and vestigal . . . . . Stage VI (megalopa)

Pandalus goniurus Stimpson
(see footnote 7)

Six larval stages.
Stages I-V, VI (megalopa), and VII (first juvenile), all from both known parentage and plankton; figures 1-7 in Haynes (1978a).
Stages I-VII from plankton; figure 2 in Makarov (1967).
Stage I, known parentage; figure 1 in Ivanov (1965).

In all stages, carapace and abdominal somites not flared laterally; subterminal seta on basipodite of maxillule. In Stages I-V, carapace usually with denticles on anteroventral margin. In Stage I, pereopods 1-5 tucked under carapace; exopodites of maxillipeds 1-3 with 4, 8, and 12 natatory setae, respectively; lacinia mobilis on left mandible; 5 spinulose spines terminally on basipodite of the maxillule; 5 setae along outer margin of scaphognathite of maxilla. Rostrum without teeth until Stage IV (in Stage III, rostrum with beginning of a tooth at base); rostral tip becomes bifid in Stage VI. Length: Stages I-VI, 3.7-15.8 mm. Range: Sea of Japan to Chukchi Sea to Puget Sound, WA; 5-450 m (Butler 1980).

Key V.—Larval and first juvenile stages of *Pandalus goniurus* (see footnote 6 and Table 4).

1. Eyes sessile; pleopods absent; telson with 7 + 7 setae . . . . . Stage I
Eyes stalked; pleopods present as minute buds; telson with 8 + 8 setae 2

2. Rostrum without teeth; pereopods 3-5 tucked under cephalothorax; uropods enclosed . . . . . Stage II
Rostrum either with undeveloped or developed teeth; all pereopods extended ventrally; uropods free 3

3. Rostrum with undeveloped tooth at its base; antennal flagellum 3 segmented and about 2/3 length of scale; endopodite of uropod about 1/3 length of exopodite . . . . . Stage III
Rostrum with ≥ 2 dorsal teeth; antennal flagellum with ≥ 6 segments and longer than scale (not including setae); endopodite of uropod nearly same length as exopodite 4

4. Rostrum with 2 dorsal teeth; antennal flagellum does not extend beyond plumose setae of antennal scale; chela of pereopod 2 not formed; width of telson increases posteriorly . . . . Stage IV
Rostrum with > 2 dorsal teeth; antennal flagellum extends beyond plumose setae of antennal scale; chela of pereopod 2 nearly or fully formed; lateral margins of telson nearly parallel or narrow posteriorly 5

5. Carapace with supraorbital spine; rostrum with 5 or 6 dorsal teeth, no ventral teeth; tip of rostrum styliform (may have undeveloped bifid tip); lateral margins of telson nearly parallel . . . . . Stage V
Carapace without supraorbital spine; rostrum with dorsal and ventral teeth; tip of rostrum bifid; lateral margins of telson narrow posteriorly 6

6. One or two setae between several posterior dorsal teeth of rostrum; 2-segmented mandibular palp without setae; exopodites of maxilliped 3 and pereopods present but reduced; carpopodite of left and right pereopods 2 with 20-25 and 7-9 joints, respectively . . . . . Stage VI (megalopa)
One or two setae between most, if not all, rostral teeth; 3-segmented mandibular palp with spiniform setae; no exopodites on maxilliped 3 and pereopods; carpopodites of left and right pereopods 2 with 29 and 11 joints, respectively . . . . . Stage VII

Pandalus hypsinotus Brandt

Seven larval stages.
Stages I-VI, VII (megalopa), and VIII-IX (juveniles), known parentage; figures 1-6 in Haynes (1976).
Stage I, known parentage; Stages II-V, from plankton; figures 5-6 in Kurata (1964a).
Stage I, known parentage; Stages II and III, from

plankton; figures 6 (only Stage I figured) in Berkeley (1930).

In all described stages, carapace without denticles on anteroventral margin; posterior margins of abdominal somites without spinules. In Stage I, thoracic appendages segmented, dactyli undeveloped; naked exopodites on pereopods 1 and 2; telson not jointed with abdominal somite 6. Beginning in Stage III, basipodite of maxillule with subterminal seta; anal spine present. Length: Stages I-VII, 5.5-12.8 mm. Range: Sea of Japan to western Bering Sea; Norton Sound to Puget Sound, WA; depth, 5-460 m (Butler 1980).

Key VI.—Larval stages of *Pandalus hypsinotus*.

1. Eyes sessile; naked exopodites on pereopods ..... Stage I
   Eyes stalked; exopodites on pereopods with natatory setae 2

2. Rostrum without teeth; uropods enclosed ..... Stage II
   Rostrum with ≥ 1 dorsal tooth at base; uropods free 3

3. Rostrum with dorsal tooth at base and no ventral teeth; exopodites on maxilliped and pereopods with natatory setae ..... Stage III
   Rostrum with ≥ 11 dorsal teeth and ≥ 2 small ventral teeth; naked, vestigial exopodites on maxillipeds and pereopods 4

4. Rostrum with 11-13 dorsal teeth and 2 or 3 small ventral teeth; tip of rostrum not bifid; mandibular palps unsegmented; telson margins nearly parallel but widen slightly posteriorly ..... Stage IV
   Rostrum with > 13 dorsal teeth and > 3 ventral teeth; tip of rostrum bifid; mandibular palp with 3 segments; telson slightly wider at midlength or narrows posteriorly 5

5. Bilobed pleopods without setae; telson slightly wider at midlength ..... Stage V
   Biramous pleopods with setae; telson narrows posteriorly 6

6. Carpopodite of left and right pereopods 2 with 19 and 7 or 8 joints, respectively; pleopods with setae only at tip; telson with 3 pairs of dorsolateral spines ..... Stage VI
   Carpopodite of left and right pereopods 2 with 24 or 25 and 10 joints, respectively; pleopods setose; telson with ≥ 4 pairs of dorsolateral spines ..... Stage VII (megalopa)

Pandalus jordani Rathbun

Thirteen larval stages.

Stages I-XIII, known parentage; figures 1-7 in Modin and Cox (1967).

Stages I-XIII, Stages XIV and XV (juveniles), all from both known parentage and plankton; figures 1-15 in Rothlisberg (1980).

Stages I-VIII, known parentage; figures 5-11 in Lee (1969).

In all described stages, carapace and abdominal somites not flared laterally and lack denticles or spinules; basipodite of maxillule without subterminal seta (except possibly Stage I). Pereopods tucked under carapace in Stage I. Rostrum without teeth in Stage I; rostrum with undeveloped dorsal tooth in Stage II; rostral tip bifid beginning at Stage VIII. Length: Stages I-XIII, 5.1-16.3 mm. Range: Unalaska, AK, to San Nicolas Island, CA; depth, 36-457 m (Butler 1980).

Key VII.—Larval and first juvenile stages of *Pandalus jordani*.

1. Eyes sessile; telson and abdominal somite 6 not jointed ..... Stage I
   Eyes stalked; telson and abdominal somite 6 jointed 2

2. Rostrum with precursor of first dorsal tooth; uropods enclosed ..... Stage II
   Rostrum with ≥ 1 movable dorsal tooth; uropods free 3

3. Rostrum with 1 movable dorsal tooth; endopodite of uropod a bud with only a few setae ..... Stage III
   Rostrum with > 1 movable tooth; endopodite of uropod > 1/2 length of exopodite and setose 4

4. Posterior width of telson about twice anterior width ..... Stage IV
   Posterior width of telson noticeably less than twice anterior width 5

5. Lateral margins of telson widen slightly posteriorly ..... Stage V

Lateral margins of telson parallel or narrow posteriorly 6

6. Rostrum with 5 developed dorsal teeth and 1 undeveloped dorsal tooth; antennal flagellum with 15 segments and same length as scale . . . . . Stage VI
Rostrum with ≥ 5 developed dorsal teeth and > 1 undeveloped dorsal tooth; antennal flagellum with > 20 segments and longer than scale 7

7. Rostrum with 5 developed dorsal teeth and styliform tip; anal spine absent . . . . . Stage VII
Rostrum with > 5 developed teeth, tip of rostrum with precursor of subterminal tooth; anal spine present 8

8. Rostrum with 7 developed teeth; lateral margin of telson with 2 spines . . . . . Stage VIII
Rostrum with > 7 developed teeth; lateral margin of telson with ≥ 3 spines 9

9. Rostrum with 9 developed teeth; inner flagellum of antennule with 3 segments; outer flagellum of antennule with 2 segments . . . . . Stage IX
Rostrum with > 9 developed teeth; inner flagellum of antennules with ≥ 4 segments; outer flagellum of antennule with 3 segments 10

10. Rostrum with 10 developed teeth; medial pair of terminal telsonic spines shorter than adjacent pair . . . . . Stage X
Rostrum with > 10 developed teeth; medial pair of terminal telsonic spines same length or longer than adjacent pair 11

11. Inner flagellum of antennule with 4 segments; medial pair of terminal telsonic spines same length as adjacent pair . . . . . Stage XI
Inner flagellum of antennule with 5 segments; medial pair of terminal telsonic spines longer than adjacent pair 12

12. Rostrum with 12 developed dorsal teeth and precursors of 3 ventral spines; terminal margin of telson straight . . . . . Stage XII
Rostrum with > 12 developed dorsal teeth and precursors of > 3 ventral teeth; terminal margin of telson convex 13

13. Carapace with supraorbital spine; pereopod 2 with unsegmented carpus . . . . . Stage XIII (last larval stage)
Carapace without supraorbital spine; pereopod 2 with segmented carpus . . . . . Stage XIV (first juvenile stage)

Pandalus kessleri Czerniavski

Four larval stages.

Stages I-IV and Stage V (first juvenile), known parentage; figures 2-6 (fig. 6, first juvenile stage) in Kurata (1955). (Stages II-IV have a mixture of zoeal and megalopal characters.)

Abbreviated larval development. In all described stages, carapace without denticles along anteroventral margin; antennal scale not jointed at tip; 2 lateral setae proximally on exopodite of maxilliped 1. Stages II and III with transverse dorsal groove. Rostrum with teeth beginning in Stage II. Supraorbital spines in Stage II only. In Stage I, antennal flagellum 3/4 length of body; antennal flagellum segmented throughout its length; telson with 30-34 setae; anal spine present; zoea longer than 8.1 mm. In Stage III, mandible with unjointed palp. Vestigial exopodites on pereopods 1 and 2 in Stages I and II. Pleopods with plumose setae in Stage II. Length: Stages I-IV, 8.1-10.8 mm. Range: Hokkaido, Japan (no depth given) (Kurata 1955).

Key VIII.—Larval and first juvenile stages of *Pandalus kessleri*.

1. Rostrum without teeth; eyes sessile . . . . Stage I
Rostrum with teeth, eyes stalked 2

2. Mandible without palp; uropods enclosed; carapace with supraorbital spine . . . . . Stage II
Mandible with palp; uropods free; carapace without supraorbital spine 3

3. Rostral tip not bifid; telson widens posteriorly . . . . . Stage III
Rostral tip bifid; telson margins parallel or narrows posteriorly 4

4. Mandibular palp unsegmented; sides of telson parallel; telson with 2 pairs of lateral spines and 11-14 terminal seta . . . . . Stage IV
Mandibular palp segmented; telson narrows posteriorly; telson with 3 pairs of lateral spines and several terminal setae vestigial as hairs . . . . . Stage V (first juvenile)

Pandalus platyceros Brandt

Five larval stages.
Stages I-V and Stages VI-X (juveniles), known parentage; figures 1-6 in Price and Chew (1972).
Stage I, known parentage; Stages II, IV?, and V?, from plankton; figures 9 and 10 in Berkeley (1930).

In all described stages, rostrum with teeth, basipodite of maxillule without subterminal seta. In Stages I-III, carapace flares laterally, lateral margins with denticles; abdominal somites flare laterally, lateral margins with spinules (Fig. 5). In Stage I, pleopods present as buds; telson jointed with abdominal somite 6. In Stages II and III, less flaring of abdominal somites and smaller denticles and spinules than in Stage I. Thoracic appendages developed in Stage I, except naked endopodites on pereopods 1-3. Length: Stages I-V, 8.1-13.0 mm. Range: Sea of Japan, Hokkaido; Unalaska Island, AK, to off San Diego, CA; depth, intertidal to 487 m (Butler 1980).

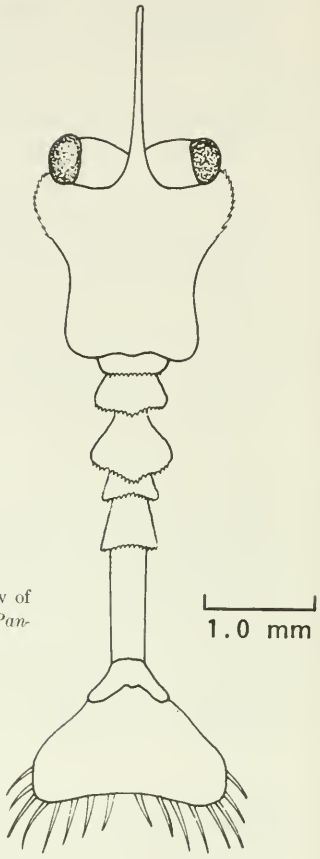

FIGURE 5.—Dorsal view of body, Stage I zoea of *Pandalus platyceros*.

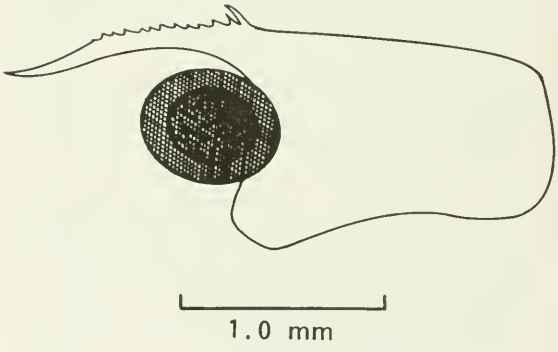

FIGURE 6.—Rostrum, Stage I zoea *Pandalus platyceros*.

Key IX.—Larval and first juvenile stages of *Pandalus platyceros*.

1. Rostrum without ventral teeth (Fig. 6); eyes sessile; pereopods with naked exopodites ..... Stage I
   Rostrum with ventral teeth; eyes stalked; pereopods with setose exopodites 2

2. Antennal flagellum with 6 segments and flagellum only slightly longer than plumose setae of scale; uropods enclosed ..... Stage II
   Antennal flagellum with ≥ 15 segments and flagellum at least twice length of scale; uropods free 3

3. Antennal flagellum about twice length of antennal scale; telson widens posteriorly; telson with 1 pair of lateral spines .... Stage III
   Antennal flagellum ≥ 3 times length of antennal scale; telson margins parallel or converge posteriorly; telson with > 1 pair of lateral spines 4

4. Carapace with supraorbital spines; mandibles without palps; pereopod 2 with unsegmented carpopodite; telson with 2 pairs of lateral spines ..... Stage IV
   Carapace without supraorbital spines; mandibles with palps; pereopod 2 with segmented carpopodite; telson with ≥ 3 pairs of lateral spines 5

5. Telson margins nearly parallel, distal margin concave ..... Stage V (megalopa)

Telson narrows posteriorly, distal margin convex ..... Stage VI (first juvenile stage)

Pandalus prensor Stimpson

Five larval stages.

Stages I-V (larvae) and VI-IX (juveniles), known parentage; figures 2-7 in Mikulich and Ivanov (1983).

Abbreviated larval development characterized by marked heterochrony in development of appendages. In all described stages, supraorbital spine absent; antennal flagellum segmented; antennal scale not jointed at tip; pereopods developed. In Stage I, rostrum curves ventrally between eyes; telson discoid and jointed with abdominal somite 6; natatory setae on exopodites of maxillipeds 1-3 and pereopods 1-2. Length: Stages I-V, carapace length 1.42-1.75 mm. Range: coastal waters of southern Okhotsk Sea, Sea of Japan, and southeastern Siberia (Vladivostok and Possjet Bay); depth, 2-93 m (Holthuis 1976; Mikulich and Ivanov 1983).

Key X.—Larval stages of *Pandalus prensor*.

1. Eyes sessile; rostrom bends ventrally between eyes ..... Stage I
   Eyes stalked; rostrum straight 2

2. Rostrum does not extend to anterior margin of eye; telson discoid; uropods enclosed ..... Stage II
   Rostrum extends beyond anterior margin of eye; telson rectangular; uropods free 3

3. Pleopods uniramous and unsegmented; telson with 7 pairs of terminal spines .... Stage III
   Pleopods (pairs II-V) biramous and segmented; telson with ≤ 5 pairs of terminal spines ... 4

4. Ventral rostrum with 4 teeth; telson with 5 pairs of terminal spines ..... Stage IV
   Ventral rostrum with 6 teeth; telson with 3 pairs of terminal spines ..... Stage V

Pandalus stenolepis Rathbun

Six larval stages.

Stages I and II, known parentage; Stages III-VII (Stage VII, first juvenile), from plankton; figures 1 and 2 in Needler (1938); figure 73 in Gurney (1942; Page 208 verifies subterminal seta on maxillule).

In Stages I-IV, carapace flares laterally, lateral margin with denticles; abdominal somites with spinules and flared laterally. Flaring, size of denticles, and spinules decrease in Stages II-IV. In Stage I, pereopods tucked under carapace; telson not jointed with abdominal somite 6; and flagellum of antenna longer than antennal scale. Pleopods absent until Stage III. Length: Stages I-VI, 6.0-14.0 mm. Range: Unalaska Island, AK, to Hecata Bank, OR; depth, 49-229 m (Butler 1980).

Key XI.—Larval and first juvenile stages of *Pandalus stenolepis*.

1. Eyes sessile; rostrum without teeth .... Stage I
   Eyes stalked; rostrum with teeth 2

2. Rostrum with only dorsal teeth (4-5 teeth); uropods enclosed ..... Stage II
   Rostrum with dorsal and ventral teeth; uropods free 3

3. Rostrum with 8 or 9 dorsal teeth and 2 ventral teeth; pleopod buds only slightly cleft ..... Stage III
   Rostrum with > 9 dorsal teeth and > 2 ventral teeth; pleopods biramous 4

4. Unjointed pleopods without setae .... Stage IV
   Jointed pleopods with setae 5

5. Right and left pereopods 2 with endopodites of same length; pleopods with a few setae; each endopodite without an appendix interna (Fig. 1N, ai) ..... Stage V
   Right and left pereopods 2 with endopodites of different lengths; pleopods setose; each endopodite with an appendix interna 6

6. Carapace with supraorbital spine; setose exopodite on each pereopod ..... Stage VI (megalopa)
   Carapace without supraorbital spine; naked, vestigial exopodite on each pereopods ..... Stage VII (first juvenile stage)

Pandalus tridens Rathbun

Probably 8 larval stages.

Stage I, known parentage; Stages I-VII, from plankton; figures 1-7 in Haynes (1976).

Stage I, known parentage; figure 1 in Ivanov (1971).

In all described stages, carapace and abdominal somites not flared laterally; antennal scale relatively long and narrow (about 5-7 times as long as wide). In Stages I-III, but rarely in Stage IV, carapace with denticles along anteroventral and posteroventral margins; posterior margin of abdominal somites 1-5 fringed with spinules (Fig. 7). Rostrum sinuate, projects somewhat upwards in Stages I-III, remains shorter than carapace as late as Stage VIII, without teeth until Stage IV. Antennal flagellum shorter than antennal scale through at least Stage V. Length: Stages I-VII, 3.1-13.0 mm. Range: Bering Sea to San Nicolas Island, CA; depth, 5-1,984 m (Butler 1980).

Key XII.—Larval stages (Stages I-VII) of *Pandalus tridens*.

1. Eyes sessile; carapace without supraorbital spine; pereopods 1-3 without exopodites; telson with 7 + 7 setae ..... Stage I
   Eyes stalked; carapace with supraorbital spine; exopodites on pereopods 1-3; telson with 8 + 8 setae 2

2. Uropods enclosed ..... Stage II
   Uropods free 3

3. Endopodite of uropod < 1/2 length of exopodite ..... Stage III
   Endopodite of uropod > 1/2 length of exopodite 4

4. Rostrum with 2 dorsal teeth; endopodite of uropod about 3/4 length of exopodite; telson widens posteriorly ..... Stage IV
   Rostrum with > 2 dorsal teeth; endopodite of uropod nearly same length as exopodite; lateral margins of telson nearly parallel 5

5. Antennal flagellum with 5 segments and about 2/3 length of antennal scale; chela of pereopod 2 slightly developed (Fig. 8); pleopod 2 about 1/4 height of abdominal somite 2 ..... Stage V
   Antennal flagellum with ≥ 20 segments and as long as or longer than antennal scale; chela of pereopod 2 well formed (Fig. 9); pleopods 2 at least 1/2 height of abdominal somite 2 6

6. Rostrum with 6 dorsal teeth; pleopods without setae; telson slightly wider near center ..... Stage VI

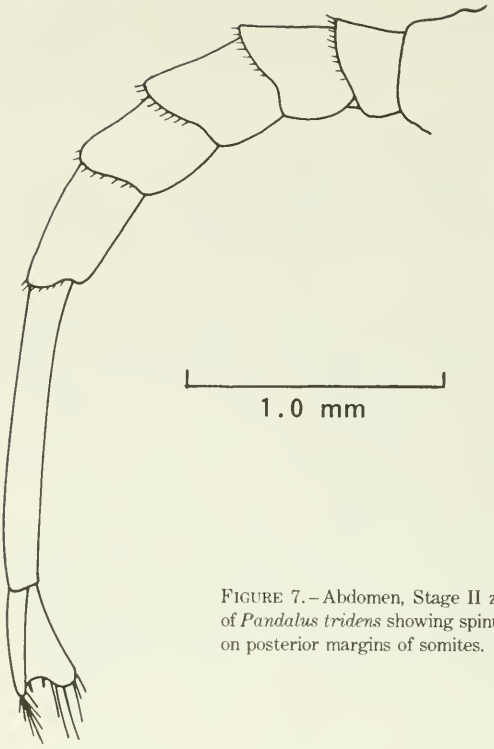

FIGURE 7.—Abdomen, Stage II zoea of *Pandalus tridens* showing spinules on posterior margins of somites.

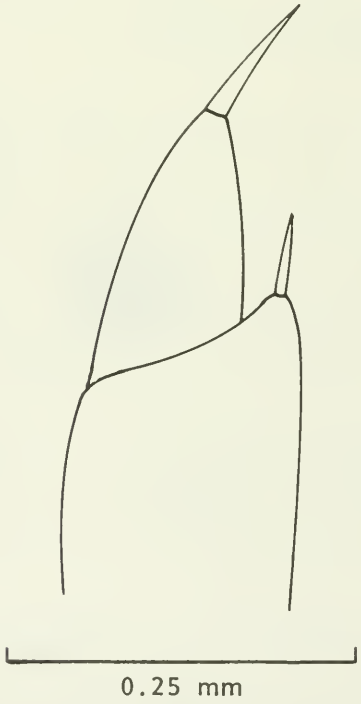

FIGURE 8.—Chela of pereopod 2, Stage V zoea of *Pandalus tridens*.

Rostrum with 7 dorsal teeth; pleopods tipped with a few setae; telson margins nearly parallel ..... Stage VII

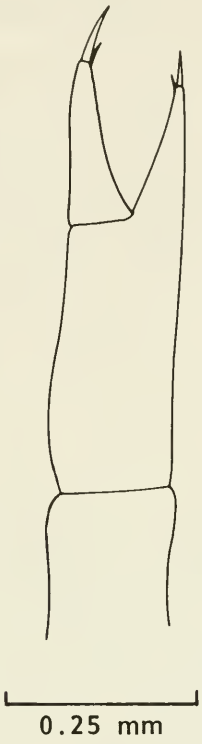

FIGURE 9.—Chela of pereopod 2, Stage VI zoea of *Pandalus tridens*.

HIPPOLYTIDAE

(Genera *Eualus*, *Heptacarpus*, *Hippolyte*, *Lebbeus*, and *Spirontocaris*)

In all described stages, rostrum absent to long, usually spiniform (slightly sinuate in species with abbreviated development); plumose seta rather than long setose spine on inner flagellum of antennule; exopodites on pereopods 1-2, 1-3, or 1-4; abdomen without dorsal spine or keels on somite 3 (megalopa of *Spirontocaris spinus* with a minute dorsoposterior spine on abdominal somite 3); posterolateral spines absent, on abdominal somites 4 and 5, or only on abdominal somite 5 (spines may be lacking in megalopa); pereopod 1 never subchelate; anal spine present in all stages (exception: at least Stage I of *Hippolyte*). Rostrum may have teeth in last zoeal stage (megalopa); supraorbital spine usually absent in Stage I. Stages I-III, antennal scale nearly always jointed or partially jointed at tip. Stage I, exopodites of maxilliped 1-3 with 4, 5, 5 natatory setae; about Stage V, setose setae on endopodite of each pleopod; telson does not widen posteriorly, has more than 1 pair of lateral spines.

The principal morphological characters and number of larval stages of known larvae of hippolytid shrimp of the northern North Pacific Ocean are summarized in Table 5.

TABLE 5.—Principal morphological characteristics and number of larval stages of known larvae of hippolytid shrimp of the northern North Pacific Ocean. + = yes; – = no; ? = unknown.

Species	Rostrum	Supra-orbital spine in Stage I	Pereopods in Stage I	Pereopods bearing an exopodite in later zoeal stages	Postero-lateral spines on abdominal somites	Telsonic spines in Stage I	No. of larval stages
Eualus barbatus	—	—	—	?	—	7 + 7	?
E. fabricii	+	—	[1]5	1-3	4, 5	7 + 7	?
E. gaimardii	+	—	[1]4	1-3	5	7 + 7	6
E. herdmani	—	—	—	?	—	7 + 7	?
E. macilentus	+[2]	—	—	?	—	7 + 7	?
E. pusiolus	+[2]	?	—	1-4	—	7 + 7	6-7
E. suckleyi	+	—	[1]5	1-3	5	7 + 7	?
Heptacarpus brevirostris	—	—	—	?	—	7 + 7	?
H. camtschaticus	+[2]	—	[1]5	1, 2	—	7 + 7	?
H. paludicola	—	—	—	?	—	7 + 7	?
H. tridens	—	—	—	?	—	7 + 7	?
Hippolyte clarki	+	—	[1]1	?	5	7 + 7	?
Lebbeus groenlandicus	+	—	5	—	4, 5	9(10) + 10(11)	3
L. polaris	+	—	5	—	4, 5	9 + 9	4
Spirontocaris arcuata	+	—	[1]5	1, 2	—	7 + 7	?
S. lilljeborgii	+	+	[1]5	1, 2	4	7 + 7	6
S. murdochi	+	—	[1]5	1, 2	4, 5	7 + 7	?
S. ochotensis	—	+	[1]5	1, 2	4, 5	7 + 7	?
S. phippsii	+	+	[1]5	1, 2	4, 5	7 + 7	6
S. spinus	+	+	[1]5	1, 2	4, 5	7 + 7	6
S. spinus var. *intermedia*	+	—	[1]5	1, 2	4, 5	7 + 7	?

[1]Undeveloped pereopods. [2]Minute.

Genus *Eualus* Thallwitz

In Stage I, rostrum absent to long; carapace without supraorbital spine; tip of antennal scale jointed; pereopods absent or, if present, undeveloped; anal spine present. Exopodites first appear on pereopods 1-3 or 1-4 in Stage III. Posterolateral spines absent, on abdominal somites 4 and 5, or only on abdominal somite 5.

Eualus barbatus (Rathbun)

Only Stage I described, known parentage; figure 3 in Ivanov (1971).

Carapace without rostrum, supraorbital spine, or denticles; pereopods absent; abdominal somites without posterolateral spines or denticles but with isolated hairs on dorsal surface of abdominal somites 3 and 4; abdominal somite 3 with indistinct row of setae on dorsal surface. Length: 4.5 mm. Range: Pribilof Islands, AK, to Hecata Bank, OR; depth, 82-507 m (Butler 1980).

Eualus fabricii (Krøyer)

Only Stages I and II described, known parentage; figure 5 in Haynes (1981).

Not "*Spirontocaris* larva Nr. 3, *Spirontocaris fabricii*?" as described by Stephensen (1916) (see Haynes 1981).

Not "*Spirontocaris*-larvae No. 3? *Spirontocaris fabricii* (Krøyer)" as described by Stephensen (1935) (see Haynes 1981).

Not *Spirontocaris fabricii* as described by Frost (1936) (see Haynes 1981).

Not "*Eualus fabricii* (Krøyer)" as described by Pike and Williamson (1961) (see Haynes 1981).

In all stages, posterolateral spines on abdominal somites 4 and 5. In Stage I, antennal flagellum about 1.5 times length of antennal scale; minute spinules along dorsoposterior margins of abdominal somites 4 and 5 (spinules absent in Stage II); supraorbital spine absent (small in Stage II). In Stages I and II, pereopods 1-3 with undeveloped exopodites. In Stage II, exopodites of maxillipeds 1-3 with 4, 9, and 11 natatory setae, respectively; telson not jointed with abdominal somite 6. Length: Stages I and II, 3.5-4.3 mm. Range: Sea of Japan, Okhotsk Sea; Chukchi Sea to British Columbia; in northwestern Alantic, from Foxe Basin and West Greenland to Massachusetts Bay (eastern United States); depth, 4-255 m (Butler 1980).

Eualus gaimardii (H. Milne Edwards)

Six larval stages.

Stages I-VI, known parentage; also Stages I and II from plankton; figure 2 in Pike and Williamson (1961).

Last zoeal stage from plankton, described as "Spirontocaris-larva No. 2A" by Stephensen (1935), probably *E. gaimardii* forma *gibba* (see Pike and Williamson 1961, p. 198). No figure.

Stage V (?), described as "*Spirontocaris* B" by Frost (1936), probably *E. gaimardii* forma *gibba* (see Pike and Williamson 1961, p. 198); figure 4 in Frost (1936).

Stage I, known parentage; described as *Spirontocaris gaimardii* by Lebour (1940); figure 1 in Lebour (1940).

Stage I, known parentage; figures 21-23 in Williamson (1957a: figures from Lebour 1940).

In all described stages, rostrum long (about 1/3 carapace length); no subterminal seta on maxillule. Rostrum without teeth until Stage V. In Stage V, rostrum with 2 dorsal teeth; in Stage VI, rostrum with 3 dorsal teeth. Supraorbital spine in Stages II-V. Carapace with 3 or 4 denticles on anteroventral margin in Stages I-IV. Antennal flagellum does not extend beyond antennal scale until Stage V. Natatory setae on exopodites of maxillipeds 1-3: 5, 7, 7 natatory setae, respectively, in Stage II; 5, 9, 9 in Stage III; and 5, 10, 10 in Stages IV and V. In Stages I-V, posterolateral spine on abdominal somite 5. Length: Stages I-VI, 2.9-5.4 mm. Range: circumpolar, southward to North Sea; Cape Cod, MA; Sitka, AK; Siberia; depth, 10-900 m (Holthuis 1947).

Eualus herdmani (Walker)

Only Stage I described, known parentage; described as "*Spirontocaris herdmani*" by Needler (1934). No figure.

Stage I, known parentage; Pike and Williamson (1961: description from Needler 1934). No figure.

Carapace without rostrum or supraorbital spine but with 3 anteroventral denticles; abdomen without posterolateral spines; anal spine minute. No length given. Range: Sitka, AK, to Puget Sound, WA; depth, 18-232 m (Butler 1980).

Eualus macilentus (Krøyer)

Only Stage I described, known parentage; figure 2 in Ivanov (1971).

No supraorbital spine; 4 denticles on anteroventral margin of carapace; pereopods absent; abdomen without spines or denticles. Length: 3.0 mm. Range: West Greenland to Nova Scotia; Bering and Okhotsk Seas; depth, 150-540 m (Holthuis 1947).

Eualus pusiolus (Krøyer)

Larvae described from Atlantic specimens.
Seven or eight larval stages.
Stage I, known parentage; Stages I-VII, from plankton; figure 3 in Pike and Williamson (1961).
Last zoeal stage, from plankton, described as "*Spirontocaris* C" by Frost (1936); figure 5 in Frost (1936).
Stage I, known parentage; described as "*Spirontocaris pusiola*" by Bull (1938); figure 1 in Bull (1938).
Stage I, known parentage; figures 27-30 in Williamson (1957a); figures from Bull (1938).

In all described stages, 3 denticles on anteroventral margin of carapace; no spines, denticles, or dorsal setae on abdominal somites. Rostrum minute in Stage I, only slightly larger in other stages, without teeth in all stages. Exopodites of maxillipeds 1-3, with 5, 8, and 8 natatory setae, respectively, in Stage II. In Stages V-VIII, pereopods 1-4 with setae. Length: Stages I-VIII, 2.2-4.8 mm. Range: Sea of Japan to Chukchi Sea and British Columbia; Gulf of St. Lawrence to Cape Cod, MA; Europe from the southwestern Barents Sea to Spain; depth, intertidal to 1,381 m (Butler 1980).

Eualus suckleyi (Stimpson)

Only Stages I and II described, known parentage; figures 3 and 4 in Haynes (1981).

In Stage I, anteroventral margin of carapace with 3 or 4 denticles; undeveloped exopodites on pereopods 1-3. In Stage II, carapace with supraorbital spine, without denticles along anteroventral margin. In Stage II, maxillipeds 1-3 with 4, 5, and 5 natatory setae, respectively; pereopods 1-5 present but undeveloped. Length: Stage I, 3.0-3.5 mm; Stage II, 3.5-4.2 mm. Range: Okhotsk Sea to Chukchi Sea to about Grays Harbor, WA; depth, 11-1,025 m (Butler 1980).

Genus *Heptacarpus* Holmes

Only Stage I described. Rostrum minute to absent; no supraorbital spine; pereopods absent or pairs 1-5 present but undeveloped; abdominal somites without posterolateral spines; exopodites develop on pereopods 1 and 2; tip of antennal scale not always jointed.

Heptacarpus brevirostris (Dana)

Stage I, known parentage; described as *Spirontocaris brevirostris* by Needler (1934). No figures.

Carapace without anteroventral spines; antennal scale partially jointed at tip. Length: Stage I, 1.5 mm. Range: Aleutian Islands, AK, to San Francisco Bay, CA; depth, intertidal to 128 m (Butler 1980).

Heptacarpus camtschaticus (Stimpson)

Stage I, known parentage; figure 8 in Haynes (1981).

Carapace without spines; minute rostrum curves slightly downward following dorsal contour of eyes; undeveloped exopodites on pereopods 1 and 2; abdomen without spines or spinules. Length: Stage I, 2.9 mm. Range: Sea of Japan to Chukchi Sea and Strait of Georgia, WA; depth, intertidal to 108 m (Butler 1980).

Heptacarpus paludicola (Holmes)

Stage I, known parentage; described as *Spirontocaris paludicola* by Needler (1934); figure 1 in Needler (1934).

Antennal scale partially jointed at tip; abdomen without posterolateral spines. Length: Stage I, 2.0 mm. Range: Tava Island, AK, to San Diego, CA; depth, intertidal to 10 m (Butler 1980).

Heptacarpus tridens (Rathbun)

Stage I, known parentage; described as *Spirontocaris tridens* by Needler (1934); figure 1 in Needler (1934).

Carapace without anteroventral spines; antennal scale unsegmented. Length: Stage I, 3.0 mm. Range: Aleutian Islands, AK, to Cape Flattery, WA; depth, intertidal to 110 m (Butler 1980).

Genus *Hippolyte* Leach

Only Stage I described. Antennal scale without joints at tip.

Hippolyte clarki Chace

Stage I, known parentage; described as *Hippolyte californiensis* by Needler (1934); figure 1 in Needler (1934).

Rostrum long; carapace with 4 anteroventral denticles; bud of pereopod 1 present; small posterolateral spines on abdominal somite 5. Length: 1.9 mm. Range: Sheep Bay, AK, to Puget Sound, WA; Santa Catalina Island, CA; depth, intertidal to 30.5 m (Butler 1980).

Genus *Lebbeus* White

In all described stages, posterolateral spines on abdominal somites 4 and 5 (Fig. 2). In Stage I, larvae relatively long (> 5.0 mm); rostrum long, slightly sinuate (Fig. 2), with no supraorbital spine. Abbreviated development.

Lebbeus groenlandicus (Fabricius)

Three larval stages.
Stages I-III from both known parentage and plankton; figures 1-3 in Haynes (1978b).
Stage I, known parentage; figure 5 in Ivanov (1971).
Not "*Spirontocaris*-larva No. 1A." as described by Stephensen (1935) (see Haynes 1978b).

Somewhat more developed in each stage than larvae of *L. polaris*. In Stage II, no vestigial exopodites on pereopods. Telson with about 20 setae in Stages I and II, and 3 + 3 spines in Stage III (megalopa). Length: 6.4-7.6 mm. Range: Sea of Japan to Chukchi Sea to Puget Sound, WA; arctic coast of Canada; Greenland to Cape Cod, MA; depth, 11-518 m (Butler 1980).

Lebbeus polaris (Sabine)

Probably 4 larval stages.
Stages I and II, known parentage; figures 1 and 2 in Haynes (1981).
Neither *Spirontocaris polaris* (= *L. polaris*) as described by Stephensen (1916) nor "*Spirontocaris*-larva No. 1" as described by Stephensen (1935) (see Haynes 1981).

In Stages I and II, telson with 9 + 9 setae. In Stage II, vestigial exopodite on peropod 1. Length: Stage I, 5.2 mm; Stage II, 5.8 mm. Range: circumpolar, southward to the Skagerrak and Hebrides; Cape Cod, MA; Bering and Okhotsk Seas; Aleutian Islands, AK; depth, 0-930 m (Holthuis 1947).

Genus *Spirontocaris* Bate

In all described stages, rostrum absent to long; posterolateral spines on abdominal somites 4 and 5, or 5 only; no minute spines on posterior margins of abdominal somites. In Stage I, supraorbital spine present or absent; all pereopods present but undeveloped. Exopodites only on pereopods 1 and 2 in later stages (usually by Stage IV or V).

Spirontocaris arcuata Rathbun

Only Stage I described, known parentage; figure 6 in Haynes (1981).

Rostrum short (about 1/7 carapace length), projects downward following contour of eyes; 2 or 3 minute denticles on anteroventral margin of carapace; supraorbital spine absent; posterolateral spines on abdominal somites 4 and 5. Length: 4.1-4.4 mm. Range: Sea of Japan to Chukchi Sea to Juan de Fuca Strait, WA; Canadian Arctic; depth, 5-641 m (Butler 1980).

Spirontocaris lilljeborgii (Danielssen)

Larvae described from Atlantic Ocean.
Six larval stages.
Stages I and II, known parentage; Stages I-V, from plankton; Stages VI (megalopa) and VII (first juvenile), reared in laboratory from Stage V; figure 1 in Pike and Williamson (1961).
Stage I, known parentage; described as *S. spinus* var. *lilljeborgi* by Lebour (1937); figure 1 in Lebour (1937).
Stage I; figures 14-16 in Williamson (1957a). Description and figures from Lebour (1937).

In all described stages, posteroanterior margins of carapace smooth; abdominal somite 4 with a dorsal tuft of short setae, without posterolateral spines. Rostrum long (about 3/4 length of antennular peduncle), deepens slightly in later stages but does not develop teeth until megalopa. Supraorbital spine rudimentary in Stage I, clearly defined in later stages. Posterolateral spines on abdominal somite 5 becoming smaller in later stages and may be absent in Stages V and VI. Megalopa and first juvenile stage without dorsal tooth on posterior margin of abdominal somite 3. Length: Stages I-VI, 4.8-8.5 mm. Range: From Spitsbergen and southwestern

Barents Sea south to south coast of England; Iceland; Greenland; east coast of North America from Nova Scotia to Massachusetts Bay; arctic Alaska; depth, 20-1,200 m (Holthuis 1947).

Spirontocaris murdochi Rathbun

Only Stages I-III described, known parentage; figures 1-3 in Haynes (in press).

Rostrum about 1/4 carapace length, supraorbital spine in Stage III; posterolateral spine on abdominal somite 5 longer than posterolateral spine on abdominal somite 4; dorsal surface of abdominal somite 4 without tuft of setae. Length: Stages I-III, 3.2-4.3 mm. Range: Arctic to southeastern Alaska, Kamchatka, Sea of Okhotsk, Patience Bay (Sakhalin); depth, 18-50 m (Holthuis 1947; Haynes in press).

Spirontocaris ochotensis (Brandt)

Only Stage I described, known parentage; figure 7 in Haynes (1981).

No rostrum; carapace usually with only 1 denticle along anteroventral margin; supraorbital spine minute; posterolateral spines on abdominal somites 4 and 5. Length: 2.8 mm. Range: Sea of Japan to Bering Sea and western coast of Vancouver Island, British Columbia; depth, intertidal to 247 m (Butler 1980).

Spirontocaris phippsii (Krøyer)

Larvae known from Atlantic Ocean.

Stage II, from plankton; Pike and Williamson (1961). No figure. Identity assumed from distribution of adults.

Stage III, from plankton; described as "*Spirontocaris*-larva Nr. 2." ("*Sp. turgida*?"); figure 6 in Stephensen (1916). Not figure 7 in Stephensen (1916), "last stage"; probably *Eualus macilentus* (see Pike and Williamson 1961) (Pike and Williamson identified figure 7 as *E. macilentus* based on identity of *S. spinus* and *S. lilljeborgii* and distribution of *Eualus* spp. in Greenland waters).

Stage V, from plankton; described as "*Spirontocaris*-larva No. 2 (? *Sp. turgida* (Krøyer))" and "*Spirontocaris*-larva No. 2B" in Stephensen (1935) (see Pike and Williamson 1961 for identification).

Spines on abdominal somites 4 and 5; abdominal somite 4 without dorsal tuft of setae. Length: Stage II, 6.0 mm. Range: circumpolar, southward to northern Norway; Cape Cod, MA; Shumagin Islands, AK; and Plover Bay, Siberia; depth, 11-225 m (Holthuis 1947).

Spirontocaris spinus (Sowerby)

Larvae described from Atlantic Ocean only.

Six larval stages.

Stages I and II, known parentage; Stages III-VII (Stage VII, first juvenile), from plankton; figure 1 in Pike and Williamson (1961).

Stage IV, from plankton; described as "*Spirontocaris* A" by Frost (1936); figure 3 in Frost (1936) (see Pike and Williamson 1961 for identification).

Stage I, probably from known parentage; Stage V, probably from plankton (see Pike and Williamson 1961); figures 17-20 in Williamson (1957a).

Larvae and juvenile stages very similar to those of *S. lilljeborgii*. In all described stages, abdominal somite 4 with a dorsal tuft of short setae; abdominal somites 4 and 5 with posterolateral spines; posterolateral spines on abdominal somite 5 remain same size in all zoeal stages. Posterior margin of abdominal somite 3 with distinct dorsal tooth in megalopa and first juvenile stage. Length: Stages I-VI, 4.3-8.0 mm. Range: Circumpolar, southward to the northern North Sea, Massachusetts Bay (eastern United States), Alaska Peninsula, and eastern coast of Siberia; depth, 16-400 m (Holthuis 1947).

Spirontocaris spinus var. *intermedia* Makarov[8]

Only Stage I described, known parentage; figure 4 in Ivanov (1971).

Not *S. spinus intermedia* as described by Makarov (1967) (see Ivanov 1971).

Rostrum long (> 1/3 carapace length); no supraorbital spine; abdominal somite 4 with dorsal tuft of setae; posterolateral spines on abdominal somites 4 and 5. Length: Stage I, 5.0 mm. Range: (see *S. spinus*); depth, 9-1,380 m (Hayashi 1977).

[8]According to Ivanov (1971), V. V. Makarov, rather than Z. I. Kobjakova, is the author of the subspecies *S. spinus* var. *intermedia* based on Article 51(e) of Chapter XI of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1964). The subspecies *S. spinus* var. *intermedia*, however, may be identical to *S. spinus*. Hayashi (1977) believed that the morphological criteria used by Kobjakova (1937) to distinguish *S. spinus* var. *intermedia* from *S. spinus* were too small and variable to be valid.

CRANGONIDAE

(Genera *Argis*, *Crangon*, *Mesocrangon*, *Paracrangon*, *Sabinea*, and *Sclerocrangon*)

Rostrum nearly always present and long (at least 1/4 length of carapace), spiniform, and always without teeth (rostrum spinulose in Stage I larvae of *Paracrangon echinata*); supraorbital spine absent; inner flagellum of antennule a setose spine or oblong projection rather than a plumose seta; tip of antennal scale never segmented; exopodite usually only on pereopod 1 (rarely on pereopod 2); maxillule without subterminal seta on basipodite; dorsal spine may be on abdominal somite 3 or keels on both abdominal somites 2 and 3; usually posterolateral spines on abdominal somite 5; endopodite of pleopods undeveloped; usually telson widens posteriorly, never with more than 1 pair of lateral spines. Pereopods 1 subchelate at about Stage V. Anal spine absent until about Stage IV.

The principal morphological characters and number of larval stages of known larvae of crangonid shrimp of the northern North Pacific Ocean are summarized in Table 6.

Genus *Argis* Krøyer

In Stage I, rostrum styliform; pereopods and pleopods developed but not functional; exopodite on pereopod 1 rudimentary or absent; abdominal somite 3 without dorsal spine; abdominal somite 5 with posterolateral spine (posterolateral spine absent in megalopa of *A. dentata*).

Argis crassa[9] (Rathbun)

Only Stage I described, known parentage; figure 2 in Ivanov (1968).

Not Stage I *A. crassa* as described by Makarov (1967) in figure 21.

Antennal scale without distal spine on outer margin; endopodite of maxillule with 5 setae; scaphognathite of maxilla with 9 setae; abdominal somites 2-5 fringed dorsally with small spinules; telson and abdominal somite 6 jointed; telson with 8 + 8 setae. Length: 7.5 mm. Range: Sea of Japan to Bering Sea to San Juan Islands, WA; depth, 4-125 m (Butler 1980).

Argis dentata (Rathbun)

Three larval stages. Stage I described, known parentage from Pacific Ocean; Stage I-III described, from plankton from Atlantic Ocean.

Stages I-III, from plankton; figures 1-6 in Squires (1965).

Stage I, known parentage; figure 3 in Ivanov (1968).

Megalopa, from plankton; described as "*Necto-*

[9]Makarov (1967) described a crangonid larva from plankton that has a short rostrum flattened dorsoventrally. He assumed it was *Argis* (= *Nectocrangon*) *crassa*. According to Ivanov (1968), who reared Stage I *A. crassa* from known parentage, the larva described by Makarov is neither *Argis crassa* nor a later stage of *Argis crassa*. The short flattened rostrum, however, is typically a postlarval (juvenile) characteristic of crangonid shrimp. The specimen described by Makarov, therefore, is probably a juvenile rather than a larva.

TABLE 6.—Principal morphological characteristics and number of larval stages of known larvae of crangonid shrimp of the northern North Pacific Ocean. + = yes; – = no; ? = unknown.

Species	Rostrum	Pereopods in Stage I	Pereopods bearing an exopodite in later zoeal stages	Posterolateral spines on abdominal somite	Dorsal spine on abdominal somite	Telsonic spines in Stage I	No. of larval stages
Argis crassa	+	5	1	5	—	8 + 8	[1]2 or 3
A. dentata	+	5	1	5	—	8 + 8	3
A. lar	+	5	—	5	—	7 + 7	[1]3
Crangon alaskensis	+	—	1	5	3	7 + 7	5
C. communis	+	[2]1	1	5	—	7 + 7	[1]5
C. dalli	+	[2]5	1	5	—	7 + 7	5
C. franciscorum angustimana	+	[2]4	1, 2	5	3	7 + 7	[1]5
C. septemspinosa	+	—	1	5	3	7 + 7	5-6
Mesocrangon intermedia	+	[2]5	1	5	—	8 + 8	5
Paracrangon echinata	+	?	1, 2	1-5	1-5	?	7 +
Sabinea septemcarinata	+	?	1	5	—	16 + 16	[1]4
Sclerocrangon boreas	—	5	—	—	—	12 + 12	2
S. salebrosa	+	5	—	5	—	22 + 22	1
S. zenkevitchi	—	5	—	—	—	—	[1]2

[1]Estimated.
[2]Undeveloped pereopods.

crangon lar?, young stage" by Stephensen (1916); figure 3 in Stephensen (1916).

In Stage I, antennal scale with distal spine on outer margin; endopodite of maxillule and scaphognathite of maxilla with 6 setae each; abdominal somites 3-5 fringed dorsally with small spinules (spinules not mentioned for Atlantic specimens); telson and abdominal somite 6 jointed; telson with 8 + 8 setae. In megalopa, short, pointed rostrum extends to middle of eye; carapace with 2 dorsal teeth, ventral edge fringed with short plumose setae; abdominal somite 5 without posterolateral spines. Length: Stages I-III, 8.0-12.0 mm. Range: Sea of Japan to Anadyr Gulf, Gulf of Georgia, and San Juan Islands, WA; arctic Canada to Nova Scotia, Canada; depth, intertidal to 2,090 m (Butler 1980).

Argis lar (Owen)

Probably 3 larval stages.
Stages I and II, from plankton; described as *Nectocrangon lar* by Makarov (1967); figure 22 in Makarov (1967).
Not Crangonidae "Species F" (described by Kurata 1964b), as assumed by Makarov (1967).[10]

In Stage I, telson and abdominal somite 6 not jointed; telson with 7 + 7 setae. In Stage II, telson with 8 + 8 setae. Abdominal somites without spinules. Length: Stages I and II, 6.2-7.5 mm. Range: Sea of Japan to Chukchi Sea to Strait of Georgia, WA; depth, 10-280 m (Butler 1980).

Genus *Crangon* Fabricius (= *Crago* Lamarck)

Five or six zoeal stages. Anteroventral margin of carapace denticulate in most if not all larval stages. In all described stages, rostrum about 1/3 carapace length, spiniform, without teeth; posterolateral spines on abdominal somite 5; exopodites develop on either pereopod 1 or pereopods 1 and 2; abdominal somite 3 usually with dorsal spine; telson always widens posteriorly, with setae and ≤ 8 + 8 spines.

Crangon alaskensis Lockington

Five larval stages.
Stages I-VII (Stage VI, first juvenile), known parentage; illustrations 1-79 in Loveland (1968).

In all described stages, rostrum barely reaches beyond eyes; dorsal spine on abdominal somite 3. Length: Stages I-V, 2.0-3.3 mm. Range: Kuril Islands; Bering Sea to Puget Sound, WA; depth, intertidal to 275 m (Butler 1980).

Crangon communis Rathbun[11]

Only Stage I described, known parentage; described as *Sclerocrangon communis* by Ivanov (1968); figure 1 in Ivanov (1968).
Not Stages II-V *C. communis* from plankton; described by Makarov (1967) as *Sclerocrangon communis*.[12]

Antennal flagellum about 3/4 length of antennal scale; antennal scale with 14 setae; abdominal somites without keels; spinules on posterior margins of abdominal somites 3-5. Length: Stage I, 4.8 mm. Range: Sea of Japan to Chukchi Sea to San Diego, CA; depth, 16-1,537 m (Butler 1980).

Crangon dalli Rathbun

Five larval stages.
Stage I, known parentage; Stages II-V and VI (first juvenile, "postlarval"), from plankton; figure 18 in Makarov (1967). Larvae figured in part but not described. Larvae thought to be identical morphologically to *C. allmani* larvae from the Atlantic Ocean (Makarov 1967).
Stage I from plankton; figures 7-9 in Birshteyn (1938).
Not "last (?) stage" as described by Birshteyn (1938) (see Makarov 1967).

Typical unabbreviated crangonid development. In all described stages, carapace without dorsal, lateral, or supraorbital spines; anterior margin of carapace denticulate; rostrum spiniform, without teeth;

[10]Morphological differences are too great for Makarov's *Nectocrangon lar* larvae and Kurata's "Species F" larvae to be identical. Makarov's larvae lack exopodites on pereopods in all stages and, in Stages I and II, have posterolateral spines on abdominal somite 5. Kurata's "Species F" larvae, known only in Stage II, have an exopodite on pereopod 1 and posterolateral spines on abdominal somites 5 and 6.

[11]Zarenkov (1965) proposed placing *C. communis* in a new subgenus, *Neocrangon*. Butler (1980) has shown that Zarenkov's diagnosis for *Neocrangon* is invalid, at least for British Columbia species. Based on Butler's findings, I have retained *C. communis* in the genus *Crangon*.

[12]It is unlikely that Makarov's (1967) larvae and Ivanov's (1968) larvae are the same species because Makarov's larvae have keels on abdominal somites 2 and 3, whereas Ivanov's larvae do not.

posterolateral spines on abdominal somite 5; abdominal somites without spinules or keels; telson always widens posteriorly, never with > 1 pair of lateral spines. In Stage V, pleopods uniramous, with buds of endopodites. Length: Stages I-V, 2.8-7.0 mm. Range: Sea of Japan to Chukchi Sea, to Puget Sound, WA; depth, 3-630 m (Butler 1980).

Crangon franciscorum angustimana Rathbun

Only Stage I described, known parentage; figure 1 in Haynes (1980b).

Rostrum extends beyond eyes; carapace without shallow transverse groove; antennal scale with 10 plumose setae including subterminal seta along outer margin; endopodite with 4 segments on maxilliped 1, and 5 segments on maxilliped 3; exopodites of maxillipeds not jointed; pereopods 1-4 present but undeveloped; buds of exopodites on perepods 1 and 2; median dorsal spine on abdominal somite 3; posterolateral spines on abdominal somite 5; fifth pair of telsonic spines about equal in length to fourth and fifth pairs. Length: Stage I, 2.8-3.3 mm. Range: Kachemak Bay, AK, to Tillamook Rock, OR; depth, 18-183 m (Butler 1980).

Crangon septemspinosa Say

Described from specimens from both Atlantic and Pacific Oceans.
Five or six larval stages.
Stages I and II, known parentage; Stages III-VI, from plankton; described as *C. affinis* by Kurata (1964b); Pacific specimens; figures 1-29 in Kurata (1964b).
Stage I, known parentage; Stages II-V, from plankton; Atlantic specimens; described as *Crago septemspinosus* Say by Needler (1941); figures 1 and 2 in Needler (1941).
Stages I-X (Stage X, first juvenile stage), known parentage (larval series likely includes extra stages); Atlantic specimens; figures 1-51 in Tesmer and Broad (1964).
Stages I-V, from plankton; Pacific specimens; figure 20 in Makarov (1967).

Discrepancies among descriptions may result, at least in part, from geographical variations in morphology. The following synopsis is based on specimens from off Hokkaido, Japan (Kurata 1964b). In all described stages, shallow transverse groove in carapace; dorsal spine on abdominal somite 3, posterolateral spines on abdominal somite 5. Exopodite only on pereopod 1. In Stage I, antennal scale with 11 setae, including 2 subterminal setae along outer margin; endopodites of maxillipeds 1-3 with 4 segments; exopodites of maxillipeds jointed; fifth pair of telsonic spines distinctly shorter than fourth or sixth pairs. Length: Stages I-V, 1.9-5.0 mm. Range: Prince Edward Island, Canada (Needler 1941); Beaufort, NC (Tesmer and Broad 1964); an estuarine, subarctic boreal species, Sea of Okhotsk (Makarov 1967); Hokkaido, Japan (Kurata 1964b); depth, 0-90 m, rarely to 440 m (Holthuis 1980).

Genus *Mesocrangon* Zarenkov

Largest larvae of Crangonidae with unabbreviated development. From Stage III on, posterior margin of telson straight or slightly concave.

Mesocrangon intermedia (Stimpson)

Five larval stages.
Stages I-V, from plankton; described as *Sclerocrangon intermedia* by Makarov (1967); figure 24 in Makarov (1967).

In Stage I, antennal flagellum about half as long as antennal scale; antennal scale with 11 setae; abdominal somites 2-3 with keels; abdomen apparently without spinules. Length: Stages I-V, 4.5-9.0 mm. Range: Sea of Okhotsk to St. Lawrence Island (Bering Sea); depth, 18-180 m (Makarov 1967).

Genus *Paracrangon* Dana

In all described stages, rostrum long, spiniform, spinulose, directed upwards about 45°; carapace with denticulate anteroventral margin; basipodite of maxilliped without subterminal seta; exopodites on pereopods 1 and 2; exopodites of pereopods 1 and 2 with ≤ 6 natatory setae; protopodite of antenna with 2 spines – one at base of flagellum, other a long spine at base of scale.

Paracrangon echinata[13] Dana

At least 7 larval stages.

[13]A diagnostic character of adult *Paracrangon* is the absence of pereopods 2 (Rathbun 1904). Kurata's (1964b) description of *Paracrangon echinata* shows pereopod 2 fully developed as late as the seventh larval stage. Either Makarov's (1967) identification of these larvae as *P. echinata* is incorrect, or *P. echinata* must have at least 3 or 4 more larval stages before pereopod 2 becomes reduced or absent.

Stages II, IV-VII, from plankton; tentatively identified as *Glyphocrangon* sp. by Kurata (1964b); figures 103-130 in Kurata (1964b).

Stages II and IV; Makarov (1967) based identity on known distribution of adults and morphology of embryo of *Glyphocrangon granulosis* (see Bate 1888); figure 28 in Makarov (1967).

Most spinose of crangonid larvae known from northern North Pacific Ocean (Fig. 10). Length: Stage II, 5 mm; Stage VII, 13.8 mm. Range: Sea of Japan; Okhotsk Sea; Port Etches, AK, to La Jolla, CA; depth, 7-201 m (Butler 1980).

Genus *Sabinea* J. C. Ross

Probably 4 larval stages. In all described stages, telson relatively wide, with shallow indentation; pereopods 2-5 without exopodites.

Sabinea septemcarinata (Sabine)

Probably 4 larval stages.

Prezoeal telson and Stages I and III, probably known parentage; Atlantic specimens: plate V, figures 1-23, and plate VI, figures 1-13, in Sars (1890).

Stages I and III, probably known parentage; described as *Crangon septemcarinatus* by Williamson (1915); figures 167-172 in Williamson (1915). Williamson's figures from Sars (1890).

Stages I and III, from plankton; figure 12, "last stage" (= Stage III), in Birshteyn (1938).

Stage I (whole larva) and Stage III (telson); origin of specimens not given; figures 1 and 2 in Williamson (1960).

Stages and origin of specimens not given, described as *Myto gaimardi* by Birshteyn (1938); plate 7, figure 1 (Krøyer 1846 in Birshteyn 1938).

In all described stages, anteroventral margin of carapace with about 7 denticles. Abdominal somites 1-4 with 1, 2, 1, and 1 ventral spines, respectively; abdominal somite 5 with posterolateral spine. Telson with 16 + 16 setae in Stage I, 13 + 13 setae in Stage III. Length: Stages I-III, 7.7-11.5 mm. Range: area of Iceland and Faroe Islands (Williamson 1960); Barents and Norwegian Seas (Williamson 1960); Chukchi Sea (Birshteyn 1938); eastern coast of North America from mouth of St. Lawrence River to Massachusetts Bay; Arctic Ocean to Point Barrow (Alaska), White Sea, and northern Europe (Williams 1974); depth, 10-240 m (Williams 1974).

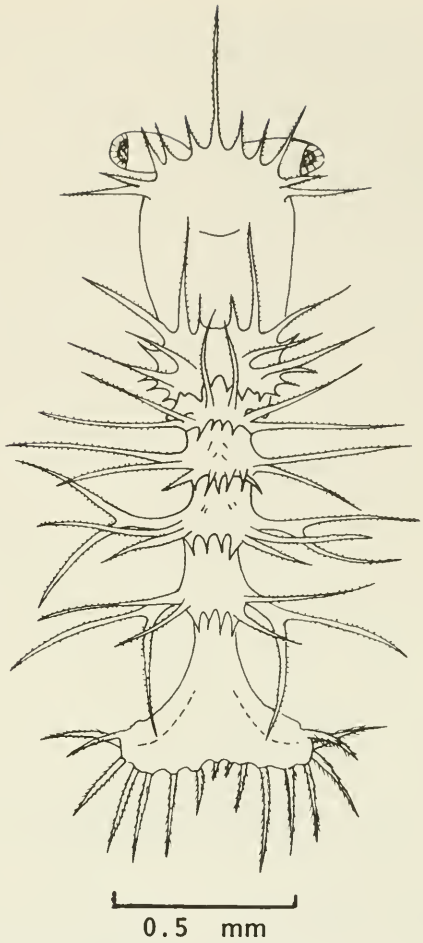

FIGURE 10.—Dorsal view of body, Stage I zoea of *Paracrangon echinata*.

Genus *Sclerocrangon* G. O. Sars

Not more than 2 larval stages. Appendages resemble adult except uropods enclosed and pleopods not fully setose. Pereopods without exopodites; pereopods 4 and 5 have characteristic sickle-shaped dactyli (Fig. 11).

Sclerocrangon boreas (Phipps)

Two larval stages.

Late embryo extracted from egg; plate VI, figures 14-28, in Sars (1890, as cited in Williamson 1960).

Stage not specified, known parentage (Makarov 1967). No figures.

Stage I and Stage II ("postlarval"), known parentage; figures 1-3 in Makarov (1968).

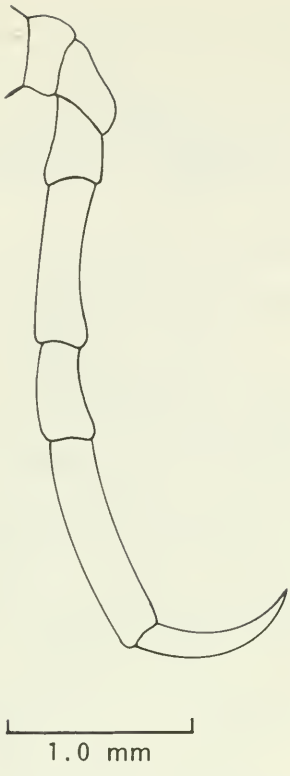

FIGURE 11.—Pereopod 4 or 5 of *Sclerocrangon* larva with characteristic sickle-shaped dactyl.

Larvae not free living but cling to pleopods of female. In all described stages, carapace without anteroventral denticles; flagellum of antennule segmented; basal portion of antennule shaped as in adult; maxillipeds with undeveloped exopodites; exopodites with a few feeble natatory setae; pereopods segmented, without exopodites. In Stage I, rostrum absent; carapace covers sessile eyes; telson and abdominal somite 6 jointed. In Stage II, rostrum short, triangular, flattened dorsoventrally. Length: Stage I, 9.0 mm; Stage II, 11.5 mm. Range: Sea of Japan to Chukchi Sea to Bare Island, WA; arctic Canada to Cape Cod, MA; North Atlantic Ocean and arctic Europe; Spitsbergen to Faroe Islands; depth, 0-366 m (Butler 1980).

Sclerocrangon salebrosa (Owen)

One larval stage.

Stage I, from plankton; figure 27 in Makarov (1967).

Embryos, from female; Stage I and Stage II ("post-larval"), from plankton; figures 1 and 2 in Makarov (1968). Larvae from plankton identified by comparison with embryos dissected from eggs.

Larvae free living. In Stage I, rostrum spiniform; carapace with anteroventral denticles; exopodites of maxillipeds fully developed, each exopodite with 5 natatory setae; telson exceptionally wide with 22 + 22 setae. Length: Stage I, 10.3-10.5 mm. Range: Okhotsk Sea; Hokkaido; no depth range (Kurata 1964b; Makarov 1967).

Sclerocrangon zenkevitchi Birstein and Vinogradov

Only Stage I described, known parentage; figure 5 in Birshteyn and Vinogradov (1953).

Carapace nearly circular laterally, without rostrum; cephalothorax and abdomen without spines or denticles; telson ovoid. Length: Stage I, 7.2 mm. Range: Bering Sea; depth, 2,995-3,940 m (Birshteyn and Vinogradov 1953).

BIOLOGY

Although pandalid, hippolytid, and crangonid larvae are common inhabitants of the neritic meroplankton of temperate and arctic waters of the North Pacific Ocean, only a few studies on their biology have been published. The most complete studies are those of Haynes (1983), Makarov (1967), and Rothlisberg (1975). Haynes described the relative abundance and distribution of pandalid shrimp larvae in the lower Cook Inlet-Kachemak Bay area, Alaska; Makarov (1967) described the distribution of decapod shrimp larvae of the West Kamchatkan shelf; and Rothlisberg (1975) discussed larval ecology of *Pandalus jordani* off the Oregon coast. In this section, I review the findings of these authors and supplement their findings with information from the literature. To avoid redundancy of citation, only information in addition to that given by Haynes, Makarov, and Rothlisberg is cited by author and date. This section does not include every known facet of the biology of decapod shrimp larvae of the northern North Pacific Ocean; however, more information can be acquired from the papers of Haynes, Makarov, and Rothlisberg and from their bibliographies.

Areas of high abundance of Stage I larvae apparently indicate areas where females are releasing larvae. For example, in Kachemak Bay in 1972, Stage I larvae of *Pandalus borealis*, *P. goniurus*, *P. hypsinotus*, and *Pandalopsis dispar* were most abundant in plankton samples collected in the same area

where females were releasing larvae (for these 4 species, females were releasing larvae at depths of about 85, 35, 50, and 100 m, respectively, based on a trawling survey).

Time of release of pandalid larvae varies with species. In Kachemak Bay in 1972, Stage I larvae of *Pandalus borealis* were not caught until the first half of April; Stage I larvae of *P. goniurus* and *P. hypsinotus* were caught later, in the latter half of April. In British Columbia waters, *P. borealis* larvae are also released earlier than larvae of either *P. goniurus* or *P. hypsinotus* (Berkeley 1930; Butler 1964).

Time of larval release is also related to water temperature. For example, a residual layer of relatively cold (sometimes subzero) water remains on the central West Kamchatkan shelf at a depth of 50-150 m throughout the summer. Decapods living in this layer of cold water release their larvae later than decapods living in warmer waters to the north and south. In the western North Atlantic Ocean, pandalid shrimp also release their larvae later in colder waters than in warmer waters (Haynes and Wigley 1969).

Depth distributions of larvae of *P. borealis* and *P. goniurus* in Kachemak Bay, 1972, were usually similar. Few larvae were in the 0-10 m stratum; most were between about 10 and 40 m. The abundance of larvae remained relatively constant below about 50 m. Numbers of Stage I *P. borealis* larvae, however, increased below about 70 m, possibly reflecting their recent release. These depth distributions differ from the depth distribution of *P. jordani* off the Oregon coast. Younger (Stages V-X) *P. jordani* larvae were found closer to the surface (0-10 m stratum) than older (Stages XI-XV) larvae (to 160 m).

Water temperature has profound effects on larval survival, growth, and size at metamorphosis. For example, survival of *P. jordani* larvae (Stages I-III) is markedly less at 17° than at 5°C. For the oldest stage (Stages IX-XIII), the relation between survival and temperature is reversed, and survival is lowest at 5°C (Rothlisberg 1979). For larvae of *P. platyceros*, survival is reduced by sudden changes in temperature, particularly about 20°C and below 9°C (Wickins 1972). At a given temperature (range 5°-14°C), growth increments for all larval stages of *P. jordani* decrease with increasing size; however, the higher the temperature, the more rapid the molting frequency (Rothlisberg 1979).

Shrimp larvae can probably influence the direction and extent of their dispersal. For instance, in Kachemak Bay, 1972 and 1976, pandalid shrimp larvae were released in the central portion of the outer bay. Some of these larvae were carried northward out of the bay in the direction of the current, but others were dispersed southwestward in a direction opposite the current. In the southern area of the western Kamchatka shelf, *Crangon* larvae released close to shore with larvae of other species, such as king crab, *Paralithodes camtschatica*, remained close to shore. Larvae of the other species, however, were carried seaward. In the northern area of the western Kamchatka shelf, where currents are faster than in the southern area, *Crangon* larvae were carried seaward (Makarov 1967). The causes for dispersal of larvae against known water currents are unknown, but dispersal may be dependent, at least in part, on the swimming capability of the larvae.

Some pandalid shrimp larvae migrate vertically in a diel cycle. In Kachemak Bay in 1972, Stages I and II larvae of *P. borealis* and *P. goniurus* were most abundant between the surface and 15 m during low light levels (1800-0800 h); however, during high light levels (1000 and 1600 h), they were most abundant between 30 and 60 m. Although present, a pronounced thermocline did not prevent larvae from moving vertically. Whether later stages of *P. borealis* and *P. goniurus* migrate similarly is unknown; however, in waters off Oregon, only Stages XII-XVI larvae of *P. jordani* migrate vertically in a diel cycle. During the day, these *P. jordani* larvae are distributed from the surface to 150 m by age: the deeper the water, the older the larvae. At night, *P. jordani* larvae migrate upwards in the water column, and the stages remain somewhat uniformly distributed with depth.

Foods of pandalid larvae have been determined during attempts to rear the larvae in the laboratory and from examination of shrimp stomachs. Larvae of *P. jordani* and *P. platyceros* have been reared on brine shrimp, *Artemia salina* nauplii (Modin and Cox 1967; Lee 1969; Price and Chew 1972), *P. hypsinotus* larvae have been reared on brine shrimp nauplii and algae (Haynes 1976), and *P. kessleri* larvae have been reared on small pieces of crab, shrimp, and mussel tissue (Kurata 1955). In 1976, I made a preliminary study (unpublished) on foods eaten by pandalid shrimp larvae in Kachemak Bay by examining their gut contents. The larvae mostly ate diatoms, especially *Coscinodiscus* types, and larval crustaceans. Many of the guts also contained black pigment and ommatidia. The assumption that pandalid larvae feed on eyes of other decapod larvae was subsequently confirmed when I observed a *P. borealis* zoea ingesting the eye of a live king crab zoea. Calcareous fragments (probably molluscs), coccolithophores, spines of larval echinoderms, and

bits of diatoms have been found in guts of *Pandalus* larvae from European waters (Lebour 1922).

Some species of pandalid larvae are sustained by their internal yolk for several days after hatching without feeding; others must feed immediately after hatching or die. *Pandalus platyceros* larvae can live 11-13 d on stored yolk with no food (Price and Chew 1972); however, when food is offered, they feed immediately after hatching. In Price and Chew's (1972) study, the starved larvae ate their dead relatives, but did not actively prey on them. Larvae of *P. jordani*, however, if not fed soon after hatching, starve and die regardless of later increases in prey concentrations (Modin and Cox 1967). In another study, 40% of Stage I zoeae of *P. borealis* without prey died in 5 d, and 100% died in 13 d (Paul et al. 1979).

The relationship between food and survival in captivity has been determined for some North Pacific Ocean larvae; however, little is known about this relationship in nature. For instance, year-class strength may be influenced or even largely determined by the quality and quantity of food available during the larval period. Unfortunately, there is virtually no information on the types and quantities of food needed for survival of shrimp larvae in nature. Until this information is available, the relation between food and survival of shrimp larvae at sea will remain unknown.

ACKNOWLEDGMENTS

Donald I. Williamson of the University of Liverpool, England, and T. H. Butler of the Pacific Biological Station, Nanaimo, British Columbia, read an earlier version of this paper and offered valuable suggestions for improvement.

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WITHIN-SEASON DIFFERENCES IN GROWTH OF LARVAL ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*

CYNTHIA JONES[1]

ABSTRACT

Data obtained from two previous studies of larval Atlantic herring growth were compared, based on otolith increment estimated age. These data, from the Gulf of Maine in 1976-77 and 1978-79, supported the hypothesis that larvae hatched early in the spawning season grew faster than larvae hatched late. Differences were significant under assumptions that increments were deposited in the otolith either daily or at 0.5 increments per day. Corroborative evidence indicated that otolith increments were formed daily at least during the early part of the spawning season.

The otolith increment technique has been used to estimate age and growth in field-caught larval Atlantic herring, *Clupea harengus harengus*, in the Gulf of Maine by Townsend and Graham (1981) and by Lough et al. (1982). Use of the increment technique to estimate age usually assumes daily deposition of otolith increments. Uncertainty exists, however, regarding increment deposition rates in the otoliths of larval herring. Gjosaeter (1981) and Øiestad (1982) have observed daily increment deposition. In contrast, Geffen (1982) found that increment deposition can be variable and a function of growth rate in larval herring, underscoring the problem in simply assuming that increments occur daily under field conditions. Growth calculations based on assumptions of daily increment deposition in populations that experience variable increment deposition rate would result in inaccurate estimates of growth rates. In most cases where otolith increment deposition has been tested under suboptimal conditions, the deposition rate has been found to be nondaily (for review see Jones 1984). Estimates of growth rates can be made, however, by expressing growth based on increment counts and with the use of corroborative evidence to determine periodicity of increment deposition.

Das (1968) found that growth rates of larval Atlantic herring, measured by following the progression of length modes over time, were different within a spawning season. He stated that early-spawned larvae grew faster than late-spawned larvae and modeled growth with curvilinear functions. Townsend and Graham (1981) also reported two different growth rates for Atlantic herring, one for larvae born prior to November 5 and one for larvae born later. Each group was modeled by two regression lines to emphasize that growth ceased in January and resumed in February. In their study, early- and late-hatched groups were analyzed separately and the comparison of growth between larvae hatched early versus late in the season was not statistically verified.

This paper uses otolith increment data from Townsend and Graham (1981) and from Lough et al. (1982) to compare early-season versus late-season larval Atlantic herring growth. The comparisons are made using the assumptions of both daily and nondaily otolith increment deposition.

METHODS

Raw data for otolith counts and larval fish lengths used in these studies were obtained from Gregory Lough of the National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA, and from Joseph Graham and David Townsend of the Maine Department of Marine Resources, Boothbay Harbor, ME. Both data sets were used in the detection of within-season differences in growth rates. Although the study of Lough et al. (1982) encompassed a larger area, only data from the Gulf of Maine were included in the analysis (Table 1), in order that comparisons were made within the same area as for Townsend and Graham (1981). Methods employed for the collection of data were reported by Lough et al. (1982) and by Lough and Bolz (1979) for the 1976-77 data and by Townsend and Graham (1981) for the 1978-79 data.

For each season (1976-77, 1978-79), data were analyzed in three ways:

[1]Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02882-1197; present address: Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, No. 3, 1985.

TABLE 1.—Station information for Atlantic herring samples from the Gulf of Maine area for the fall and winter of 1976-77 sampling program. (Data from Lough et al. 1982.)

Vessel	Cruise No.	Stn.	Lat. N	Long. W	Date	Time (Night or Day)
Annandale	76-01	38	43°37′	69°22′	8 Oct.	0300 (N)
		44	43°44′	68°50′	8 Oct.	1415 (D)
		59	44°25′	67°35′	9 Oct.	1515 (D)
		65	44°36′	67°07′	13 Oct.	0330 (N)
Researcher	76-01	102	42°58′	70°00′	8 Dec.	1030 (N)
		105	43°30′	69°30′	9 Dec.	1100 (N)
Mt. Mitchell	77-01	122	43°14′	70°01′	24 Feb.	1620 (D)
		123	43°00′	70°15′	24 Feb.	1933 (D)

1) Hatch date was calculated on the assumption of daily increment deposition, and all data were considered.
2) Hatch date was calculated on the assumption of daily increment deposition only with larvae which had 60 or fewer increments included for analysis. This was done to determine whether growth differences were present in the earlier months of life. Also, since the range of increment counts for the late-hatched larvae from 1976 to 1977 was greater than for early-hatched larvae, use of a truncated data set resulted in more valid comparisons.
3) Hatch date was calculated on the assumption of nondaily deposition (0.5 increment/d).

Date of hatching was calculated by subtracting the estimated age of each larva from its date of capture. This calculation, of course, depends on how age was estimated. According to the Lough et al. (1982) calculation, a larva with 10 otolith increments would be 29 d old: 22 d for the first 3 increments, plus 7 d to lay down the next 7 increments. According to the assumptions used by Townsend and Graham (1981), a larva with 10 otolith increments would be 15 d old, assuming that increment deposition began 5 d after hatch, and was daily thereafter. There is a difference of 14 d between these two estimates of age, and, therefore, estimated day of hatch. This does not affect the regression analysis, as long as the independent variable used is increment count, not age.

The range of possible hatch dates for each individual was also calculated, based on the consideration that deposition rates could vary from 0.5 to 1.0 increment/d (after Geffen 1982). Age could be equal to the number of increments plus a constant (5 d) or up to twice the number of increments plus a constant (5 d).

Larvae were classified as either early- or late-hatched within the spawning season. For 1976-77 the early-late division date was placed at the discontinuity in the frequency of hatching plot, which also occurred at the midpoint in the spawning cycle. Division date for the 1978-79 data set was placed at approximately the division of Townsend and Graham (1981) which they felt represented two different groups of larvae.

For analysis of nondaily deposition, the data were partitioned to insure that there could be no overlap of early- and late-hatched classification of larvae, assuming deposition ranged from daily deposition to deposition of one increment every 2 d. Any late-hatched larva whose possible range of hatch dates overlapped the division date (for early-hatched vs. late-hatched classification) was eliminated from analysis. This resulted in a loss of data (e.g., the fish whose possible hatch date overlapped the division date) and decreased the ability to detect differences.

Ordinary least squares linear regressions were fit to each data set. Bartlett's test for homogeneity of variance (Ostle and Mensing 1975) was applied to the data before each analysis. After regressions were fit, the residuals of length were plotted against predicted length and examined for trends (Draper and Smith 1981). *F*-tests (Ostle and Mensing 1975) were applied to paired linear regressions, early-hatched versus late-hatched, to determine whether the slopes were significantly different. This test showed whether the data were better fit by two lines, one for early-hatched and one for late-hatched larvae, or whether a single regression line was preferable. In the regression plots the change in length is expressed in millimeters per increment.

The von Bertalanffy growth equation,

$$L_t = L_\infty (1 - e^{-k(t - t_0)})$$

was also fitted to the data, using the nonlinear regression procedure (NLIN) within SAS (Statistical Analysis Systems, SAS Institute, Cary, NC). Estimates of the parameters (K, L_∞, t_0) of the von Bertalanffy equations for early- and late-hatched larvae were compared with a Fisher-Behrens test (Hoenig 1982) to determine whether the vector of parameter estimates from the two classifications was significantly different.

RESULTS

Linear regression models fitted to larval length-at-increment count data showed significant differences between larvae hatched early and late in the spawning season. Larvae hatched early had achieved greater length at a given increment count than those

hatched later. Intercepts were not compared since the data sets did not contain any larvae with fewer than seven increments and inferences outside the range of the data should not be drawn.

1976-77 Study

A frequency plot of hatching dates for the Gulf of Maine stations is shown in Figure 1 for age estimated on the assumption of daily ring deposition and in Figure 2 for age estimated on the assumption that deposition was daily or as little as one ring every other day.

Differences in length-at-increment count between early- and late-hatched larvae was striking (Table 2). Regression plots are shown in Figure 3. Analysis of the data confirmed that the length-at-count data were modeled more accurately by two different regression lines ($P < 0.01$) and that the slopes of these two regressions were significantly different (P

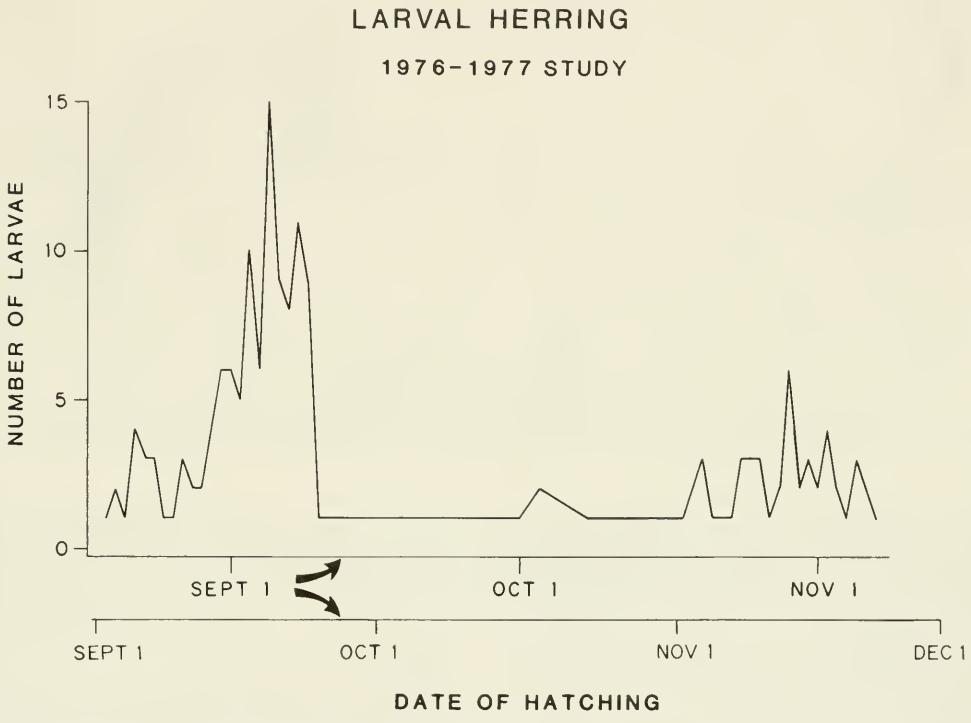

FIGURE 1.—Frequency of Atlantic herring hatching during the 1976-77 study. Upper scale gives the day of hatch based on the Lough et al. (1982) aging method, or, as discussed in the text. Lower scale gives the day of hatch based on Townsend and Graham's (1981) aging method as discussed in the text. Arrow indicates division point between early- and late-hatched classification.

TABLE 2.—Regression analysis of 1976-77 Gulf of Maine Atlantic herring data. (Data from Lough et al. 1982.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	64	15.8	0.0948	0.0047	0.87		
60 or fewer	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	44	14.6	0.1470	0.0274	0.41		

Data were classified into early- and late-hatched larvae. These two groups were compared by fitting ordinary least squares regression lines to 1) all the data within the two classifications, and 2) using only lengths from larvae with 60 or fewer increment counts. Slopes and intercepts were compared between early versus late for each group.

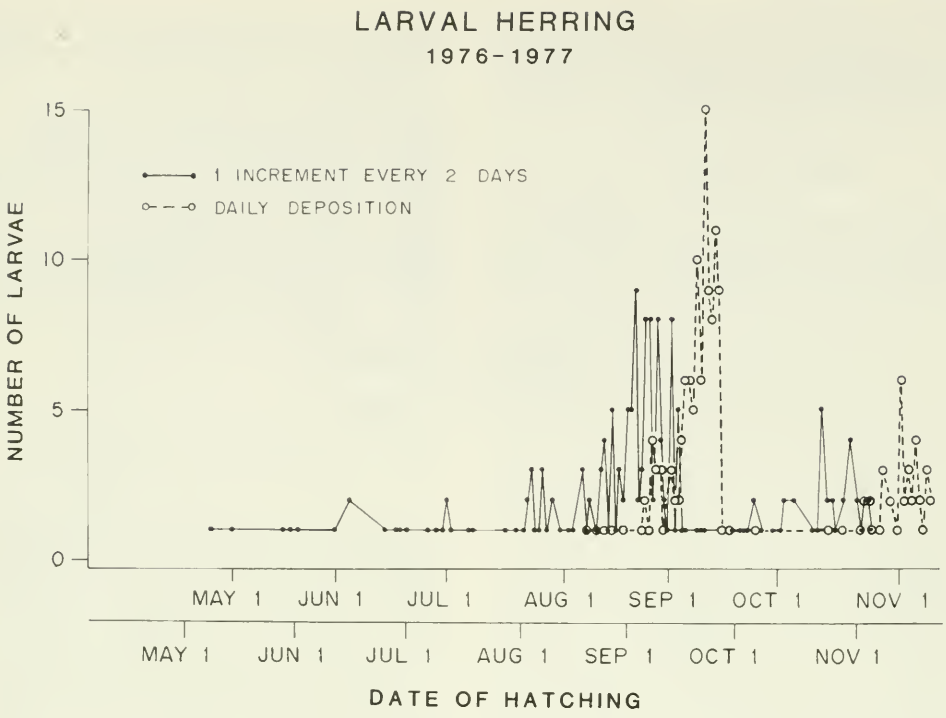

FIGURE 2.—Frequency of Atlantic herring hatching during the 1976-77 study, calculated under two assumptions of otolith increment count and age relationship.

< 0.01). The average length achieved per increment was 0.33 mm and 0.10 mm for early- and late-hatched larvae, respectively. Bartlett's test confirmed that variances were homogeneous. Analysis of residuals showed that the last three residuals, corresponding to the three largest larvae, were below the average. The exclusion of these points did not alter the results of the analysis.

Analysis of the subset of larvae with fewer than 60 increments (Table 2) showed that data were better fitted with two different regression lines ($P < 0.01$) and that the slopes were significantly different ($P < 0.01$). Regression plots are shown in Figure 4. Change in length of early-hatched larvae was 0.33 mm/increment and 0.15 mm/increment for late-hatched larvae. Bartlett's test showed variances to be homogeneous and residuals showed no trends, except for the two youngest late-hatched larvae which fell below the regression line. Late-hatched larvae were slightly larger than early-hatched larvae for the lowest increment counts.

Differences in length-at-increment count were apparent for data whose calculated hatch dates included deposition rates of from 0.5 to 1.0 increments/d (Table 3). The change in length of early-hatched larvae was 0.33 mm/increment compared with 0.17 mm/increment for late-hatched larvae. Data were again better fit with two regression lines ($P < 0.01$) whose slopes were significantly different ($P < 0.01$).

The von Bertalanffy growth equation fit the late-hatch larval data well (Table 4). L_∞ was estimated at 29.81 mm, with a 95% confidence interval of 26.41 to 33.22 mm. Fit to the early-hatched larval data was poor. L_∞ was estimated at 35.59 mm, with a confidence interval of 17.76 to 53.41 mm. These data were adequately fit with a straight line, and there is little justification for fitting with a curvilinear function other than it has been traditionally used for adult fish. Beverton and Holt (1954), however, stated that the von Bertalanffy equation should not necessarily be used during the early life stages. Nevertheless, when the parameter estimates from the two curves were compared, they were signifi-

FIGURE 4.—Regression plot of length-at-otolith increment count for Atlantic herring. Only lengths for larvae with 60 or fewer otolith increments have been included for analysis. Data from Lough et al. (1982).

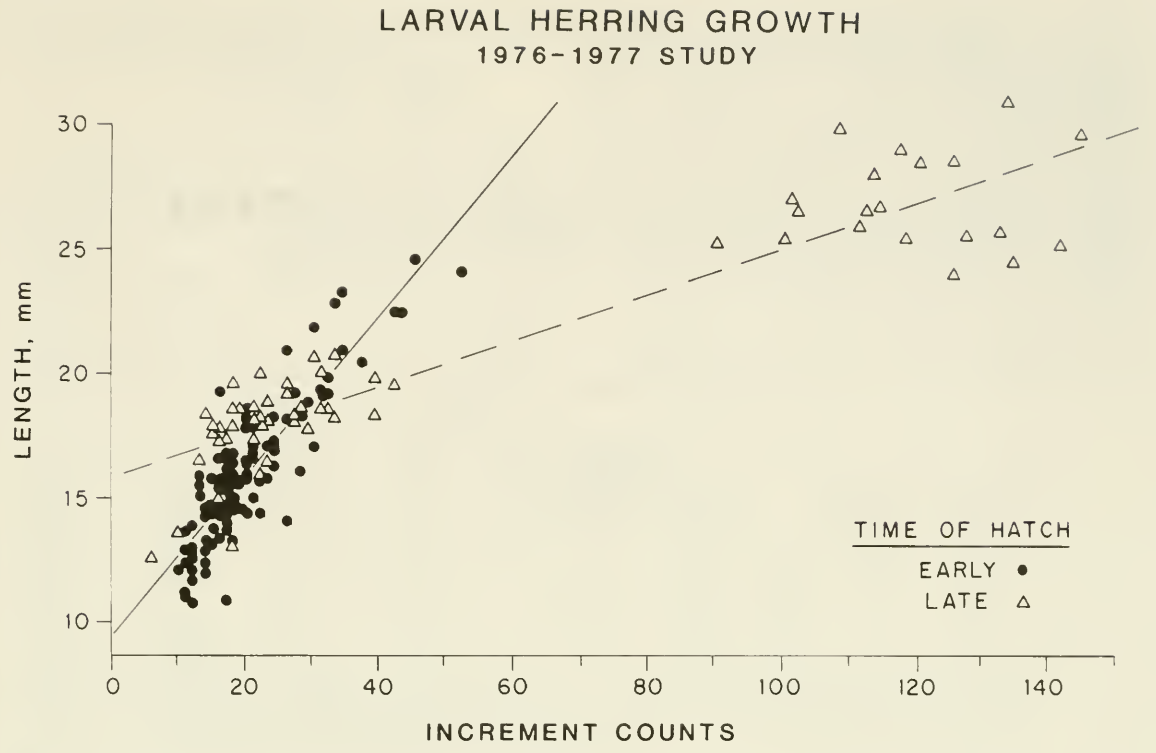

FIGURE 3. – Regression plot of length-at-otolith increment count for Atlantic herring. Complete data set represented. Data from Lough et al. (1982).

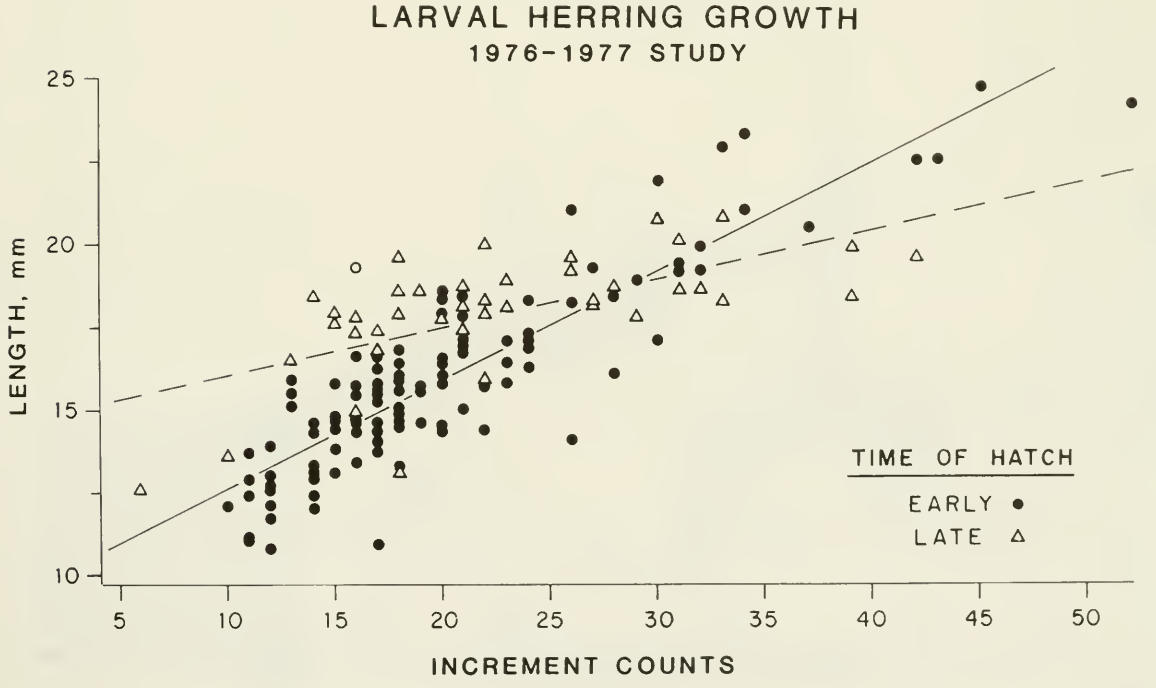

TABLE 3.—Regression analysis of 1976-77 Gulf of Maine Atlantic herring data based on two otolith increment deposition assumptions. (Data from Lough et al. 1982.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope of regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	39	14.2	0.1711	0.0364	0.37		

Legend: Data were classified into early- and late-hatched larvae. Two dates of hatch were calculated: 1) Age equalled increment count plus a constant, and 2) age equalled twice the increment count plus a constant. This resulted in a range of potential hatching dates. Any late-hatched larva whose range of hatch date overlapped the division date (Text Fig. 1) was eliminated from the analysis.

TABLE 4.—Estimation of von Bertalanffy growth parameters for larval Atlantic herring from the Gulf of Maine.

Year	Hatch classification	Parameter	Estimate of parameter	Standard error of estimate	95% confidence interval	
					Low	High
1976-77	Early	K	0.01865	0.00939	0.00008	0.03723
		L_∞	35.6	9.0	17.8	53.4
		t_0	−12.3	5.00	−22.2	−2.41
	Late	K	0.01530	0.00457	0.00616	0.02443
		L_∞	29.8	1.7	26.4	33.2
		t_0	−38.01	12.46	−69.92	−13.10
1978-79	Early	K	0.00262	0.00158	−0.00050	0.00575
		L_∞	113.2	48.8	16.3	210.1
		t_0	−42.28	9.94	−62.00	−22.57
	Late (convergence criteria could not be met)					

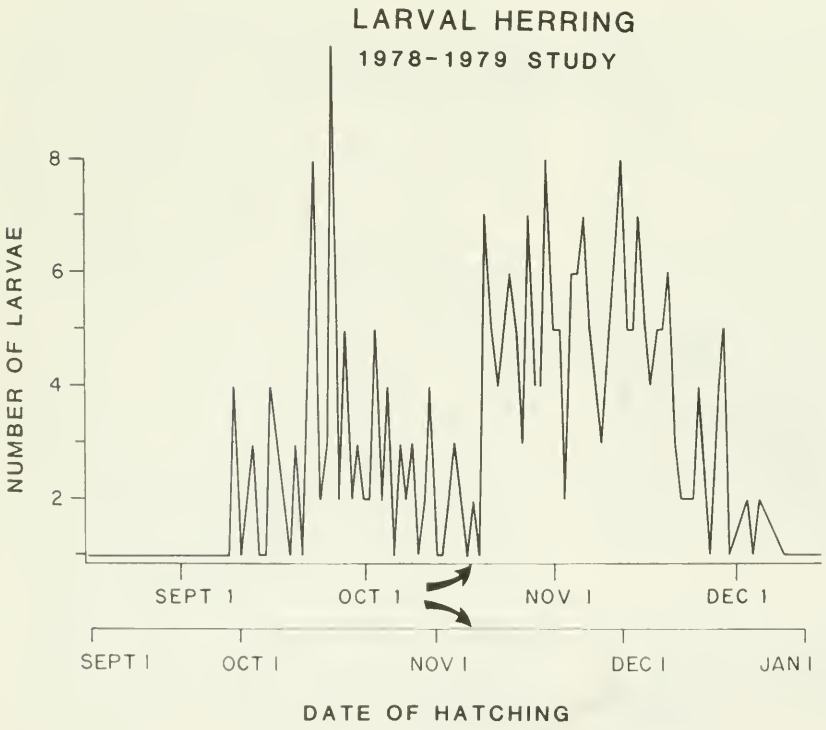

FIGURE 5.—Frequency of Atlantic herring hatching during the 1978-79 study. Upper scale gives the day of hatch based on the Lough et al. (1982) aging method as discussed in the text. Lower scale gives the day of hatch based on Townsend and Graham's (1981) aging method as discussed in the text. Arrow indicates division point between early- and late-hatched classification.

cantly different ($P < 0.01$)—early-hatched larvae grew faster than late-hatched larvae.

1978-79 Study

A frequency plot of hatching dates under the assumption of daily increment deposition for larvae sampled in the Sheepscot estuary is shown in Figure 5.

Analysis (Table 5) showed that the data were better fit with two lines ($P < 0.01$) and that the slopes were different ($P < 0.01$). The change in length was 0.21 mm/increment and 0.18 mm/increment for early- and late-hatched larvae, respectively (Fig. 6). However, the results should be interpreted with the knowledge that Bartlett's test showed the variances to be heterogeneous. This could have been caused by actual heterogeneity of variances, or by nonnormality in the data. The F tests used in these analyses assumed equal variances between the hatch classifications. Cochran (1947) reported, however, that lack of homogeneity would decrease the power of an F test to discern true differences when they did, in fact, occur. Since differences were statistically significant, not meeting this assumption did not hinder analysis (the use of various transformations

TABLE 5.—Regression analysis of 1978-79 Gulf of Maine Atlantic herring data. (Data from Townsend and Graham 1981.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope of regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	102	13.3	0.2134	0.0661	0.92	<0.01	<0.01
	Late	198	14.2	0.1793	0.0060	0.82		
60 or fewer	Early	42	9.4	0.3378	0.0189	0.89	<0.01	<0.01
	Late	53	11.4	0.2434	0.0203	0.74		

Data were classified into early- and late-hatched larvae. These two groups were compared by fitting ordinary least squares regression lines to 1) all the data within the two classifications, and 2) using only lengths from larvae with 60 or fewer increment counts. Slopes and intercepts were compared between early vs. late for each group.

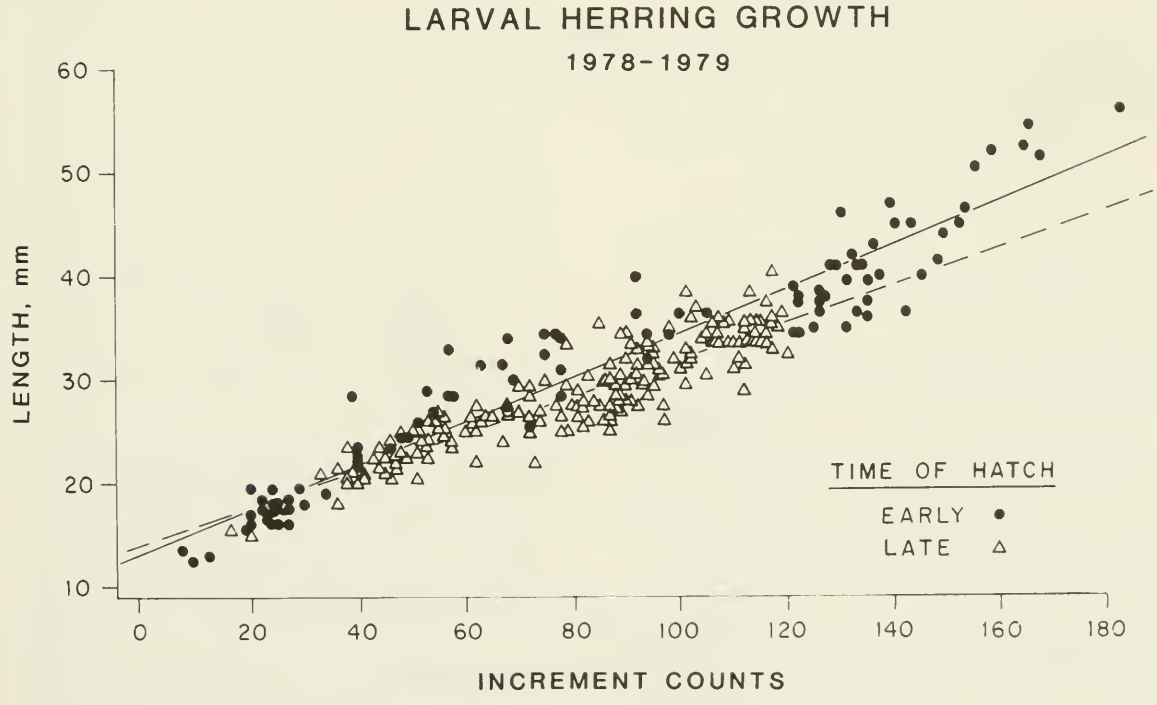

FIGURE 6.—Regression plot of length-at-otolith increment count for Atlantic herring. Complete data set represented. Data from Townsend and Graham (1981).

did not result in homogeneity of variances). Except for the residuals for three small larvae, analysis for residuals showed no trends.

For larvae with 60 increments and fewer (Fig. 7), Bartlett's test showed homogeneity of variance. These data were better fitted by two lines ($P < 0.01$); the slopes were significantly different ($P < 0.01$). The change in length was 0.34 mm/increment and 0.24 mm/increment for early- and late-hatched larvae, respectively.

The von Bertalanffy growth equation fit the early-hatched larval data poorly (Table 4). L_∞ was estimated at 113.22 mm, with a 95% confidence interval of 16.37 to 210.06 mm. The von Bertalanffy growth function could not be fitted (solution would not converge) to the late-hatched larval data.

The 1978-79 data could not be tested under assumptions that increment deposition could vary from 0.5 to 1.0 increment/d. Almost all of the calculated hatch dates for late-hatched larvae, estimated on deposition rates of 0.5 increment/d, overlapped the classification division date. Too few points were left for analysis.

DISCUSSION

Evidence from the Gulf of Maine supports the hypothesis that increase in length for herring larvae hatched early in the spawning season is greater than for larvae hatched late in the season. These differences were evident both under assumptions of daily otolith increment deposition and for deposition of one increment every other day. Before these differences are assumed to be due to differences in growth, however, there are other hypotheses which should be considered that could explain these observations. Differences could be the result of within-season changes in otolith increment deposition rates, or of differential mortality due to selective predation.

If there are within-season changes in otolith increment deposition rates, growth (change in length at age) could actually be similar, but the calculated growth rates would appear to be different because they are expressed as change in length per increment count. In order for this hypothesis to explain the above results, larvae born early in the season would be required to put down fewer increments per time period than would larvae born late in the season. The data allow a test of the hypothesis that larvae lay down fewer than 1 increment/d during the early part of the year. When estimated hatching dates are calculated for larvae caught early in the season, under the assumption that one increment was deposited every other day, some of these larvae

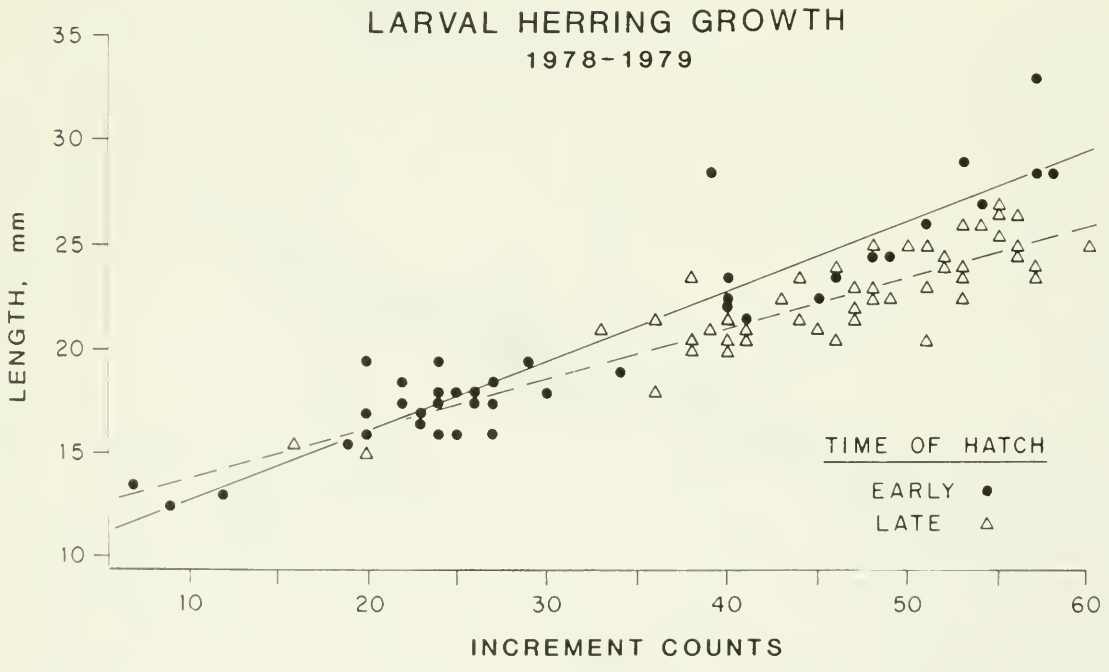

FIGURE 7.—Regression plot of length-at-otolith increment count for Atlantic herring. Only lengths for larvae with 60 or fewer otolith increments have been included for analysis. Data from Townsend and Graham (1981).

would have had to appear in the plankton in the middle of the summer (Fig. 3). However, newly hatched larvae are not found in significant numbers in the plankton before September (Boyar et al. 1973; Colton et al. 1979). It is far more plausible that larvae hatched early in the season, when growing conditions are more nearly optimal (Sherman and Honey 1971; Cohen and Lough 1983), deposit increments with close to daily periodicity. Hence, in order for this hypothesis to be true, late-hatched larvae would have to deposit increments at a rate greater than 1 increment/d. There is no evidence in the literature to support this for larval herring.

Difference in population growth rates within a spawning season could also result from a shift in size-specific mortality during the season. The observed differences in growth rate could result if early-hatched larvae have higher cumulative mortalities for slower growing individuals, while late-hatched larvae have higher mortalities for faster growing individuals. Progressively, fewer and fewer of the selectively predated larvae would be seen in older ages. This would result in differences in population growth rates that are not apparent for individuals within the population.

Although differential mortality cannot be dismissed with the available data, the most plausible explanation for the differences in length-at-increment count is an actual difference in larval growth rate over the spawning season. Such differences in population growth rate can be important for larval herring survival. Since greater time spent in the larval stage is thought to be related to increased mortality, it is interesting to note that an early-hatched larva from the 1978 study would require, on the average, 80 d to reach 30 mm, compared with 88 d for a late-hatched larva. For the 1976 study, it would take, on the average 63 d for an early-hatched larva to reach 30 mm compared with 157 d for a late-hatched larva to reach this size.

It has been shown that in both years, late-hatched larvae are larger than early-hatched larvae at the time of first increment formation. This could result from larger eggs being produced in the winter (Cushing 1967), or from different growth rates from hatch to the age of larvae covered in this study. Without further evidence of differences in egg size or actual growth rates between hatch and the age these studies began, neither hypothesis can be supported.

Differences in growth rate within the spawning season can contribute to error when using an age-length key to age larvae. For a given length, samples containing early-hatched larvae would yield different ages than samples containing late-hatched larvae. For the 1978-79 study (under the assumption of daily increment deposition), a 25 mm larva would average 60 increments for early-hatched larvae versus 56 for late-hatched larvae. For the 1976-77 study a larva of this length would average 47 versus 102 increments, respectively. This additional variation should be taken into consideration when using age-length keys for larvae.

Differences in growth during the spawning season might be due to changes in the environment when a species of fish spawns over a protracted time period, such as Atlantic herring which spawns from late August through November (Boyar et al. 1973; Colton et al. 1979). Early in the season copepods, the main food for larval herring (Sherman and Honey 1971; Cohen and Lough 1983), are more abundant than late in the spawning season (Sherman et al. 1983). Temperatures average 12°-16°C early in the season and < 8°C later in the season (Colton 1968; Colton and Stoddard 1972). Day length and metabolic demand may also vary over the spawning season. Alternately, differences in growth between larvae hatched early and late in the season could be the result of genetic differences if early and late spawners are from different stocks.

ACKNOWLEDGEMENTS

I thank R. G. Lough, D. Townsend, and J. J. Graham for providing their data; and B. E. Skud, R. G. Lough, J. J. Graham, and K. R. Hinga for their suggestions and review of this manuscript.

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SEASONAL CYCLES OF FAT AND GONAD VOLUME IN FIVE SPECIES OF NORTHERN CALIFORNIA ROCKFISH (SCORPAENIDAE: *SEBASTES*)

PATRICK J. GUILLEMOT,[1] RALPH J. LARSON,[2] AND WILLIAM H. LENARZ[3]

ABSTRACT

Seasonal changes in visceral fat volume and gonad volume are compared in five species of rockfish from northern and central California: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. In these species, visceral fat was deposited between spring and fall, at the same time as gametogenesis. Visceral fat declined in volume between fall and spring, coinciding with the decline in volume of testes and preceding the release of embryos in females. We suggest that increased feeding during the summer upwelling season provides the energy for simultaneous fat accumulation, gametogenesis, and perhaps somatic growth. During subsequent seasons of presumed food storage, these rockfishes may utilize visceral fat reserves for maintenance. This pattern of fat deposition and utilization may contribute to the long life and repeated reproduction of rockfishes, at the expense of current fecundity and growth.

Our data also suggest that rockfishes which spawn only once during the reproductive season have fat cycles of greater magnitude than those spawning more than once a year. Of the species that we studied, the apparent single spawners *S. entomelas* and *S. flavidus* have more northerly geographic distributions and larger fat cycles than the multiple spawners *S. goodei* and *S. paucispinis*. It is possible that the shorter and more pronounced productive season in the north leads to a greater need for fat reserves during winter and makes the wintertime production of additional batches of eggs energetically difficult.

The seasonal storage and utilization of lipid (and nonlipid) reserves are important in the metabolic activities and overall life histories of many animals (Love 1970; Shul'man 1974; Derickson 1976a and associated papers). While cycles of lipid storage and utilization are generally associated with seasonal changes in food availability (Derickson 1976b) or metabolic demands (Lawrence 1976), the functions of lipid storage are varied.

In many fishes, reserves are used primarily in reproduction, as indicated by complementary cycles of lipid content and reproductive activity (Lasker 1970; Shchepkin 1971a, b; Schevchenko 1972; Shul'man 1974; Tyler and Dunn 1976; Wootton and Evans 1976; Lasker and Smith 1977; Diana and MacKay 1979; Delahunty and de Vlaming 1980; Patzner 1980; Hunter and Leong 1981). The seasonal accumulation of sufficient reserves may be a prerequisite for sexual maturity in some fishes (Iles 1974), and the amount of material stored may influence fecundity (Tyler and Dunn 1976). Reserves may also be used in migration (Robertson and Wexler 1960; Dotson 1978; Glebe and Leggett 1981 a, b), and, when used in spawning migrations, may contribute indirectly to reproduction.

Slobodkin (1962) and Calow (1977), however, noted that fat deposition may actually detract from reproduction, particularly when fat deposition and reproduction are concurrent. In such cases, reserves are often used instead for maintenance during periods of food scarcity (Calow and Jennings 1977), enhancing the opportunity to reproduce in the future. Some fishes seem to use reserves both for reproduction and maintenance, when spawning occurs during periods of food scarcity or fasting (Wilkins 1967; MacKinnon 1972; Iles 1974; Newsome and Leduc 1975; Foltz and Norden 1977; Dawson and Grimm 1980; Pierce et al. 1980; Glebe and Leggett 1981 a, b). The interpretation of such cases is complex, since reproduction and maintenance may be competing concurrently for reserves.

Roberts (1979) noted that fat was deposited seasonally around the viscera of two species of shallow-water rockfish, *Sebastes mystinus* and *S. melanops*. He suggested that the cycle of fat deposition and utilization was related to seasonal changes in the abundance of food and to reproduction.

In this paper we examine the seasonal relationship

[1]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA; present address: 3298 Madera Avenue, Oakland, CA 94619.

[2]Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132.

[3]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

Manuscript accepted August 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

between visceral fat volume and gonad volume in five offshore species of rockfish: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. Based on Roberts' suggestion and the general literature on fat cycles in fishes, we expected to find complementary cycles of fat and gonad volume, indicating that reserves are used in reproduction. We used visceral fat volume as a convenient index of the timing and magnitude of seasonal changes in reserves, explicitly assuming that reserves stored elsewhere would change coincidentally (Delahunty and de Vlaming 1980). Since we did not measure total reserves, our data on visceral fat volume cannot be applied to quantitative studies of energy budgets, but are most useful for examining seasonal changes and making comparisons within a group of closely related species.

The use of gonadal volume as an index of reproductive activity requires some explanation. In males, gonadal volume is a good index of the timing of gametogenesis. In females of this live-bearing genus, however, gametogenesis is often reflected only in the initial increase of gonadal volume. Following fertilization (which may occur some time after copulation, due to sperm storage [Sorokin 1961; Echeverria 1981[4]; Boehlert and Yoklavich 1984]), ovarian volume continues to increase during a gestation period that lasts a month or so (Moser 1967). There may be some postzygotic nutrition of embryos during this time (Boehlert and Yoklavich 1984), but much of the increase in volume is due to the accumulation of water (Moser 1967). In some species of *Sebastes* that spawn more than once a year, gametogenesis takes place again late in the reproductive season of females. Among the species considered here, *S. paucispinis* and *S. goodei* are clearly multiple spawners (Moser 1967; MacGregor 1970), and Echeverria[5] has presented some evidence for multiple spawning in *S. pinniger*.

MATERIALS AND METHODS

Party boat and commercial rockfish catches were sampled weekly, as a part of a large-scale study, by personnel from the National Marine Fisheries Service (Tiburon Laboratory) and the California Department of Fish and Game, at northern California fishing ports between Crescent City (lat. 41°N) and Morro Bay (35°N). The species sampled depended on the day's catch. Samplers measured the total length of each specimen to the nearest millimeter and removed the viscera and gonads for preservation in 10% Formalin[6] in seawater.

In the laboratory, fat tissue was dissected from the viscera and its volume estimated by water displacement in graduated cylinders. In some samples, a small amount of fat had liquified. The volume of this liquid was estimated and added to total fat volume. Gonads were also removed and their volume measured as above. The state of development of ovaries and testes was scored according to indices based mainly on gonad morphology and coloration (Moser 1967; Gunderson et al. 1980). Histological preparations of small gonads were used to confirm sex and state of maturity. Data for species, sex, total length, stage of maturity, and fat and gonad volume were stored using a computer.

Data on visceral fat volume were analyzed for collections made between March 1980 and February 1981, inclusive. Measurements of gonad volume were begun in June 1980 and continued until May 1981 to obtain a full year of data. For each species, data were pooled over all ports of collection and divided quarterly, as follows: spring (March-May), summer (June-August), fall (September-November), and winter (December-February). Quarterly division of data gave good sample sizes for most seasons, yet still allowed seasonal separation. Primary production is relatively low off California during fall and winter, but is greater during most of spring and summer, when coastal upwelling occurs (Bolin and Abbott 1963).

To facilitate comparisons, visceral fat volume and gonad volume were expressed as log-transformed power-function regressions of volume on fish length. The power equation is:

$$V = aL^b,$$

where V is volume, L is total length, and a and b are estimated parameters. This equation is often used to express the relationship between volumetric measures, such as fecundity, and linear measures, such as length (Bagenal 1978; Glebe and Leggett 1981a; de Vlaming et al. 1982). Logarithmic transformation to

$$\ln V = \ln a + b \ln L$$

[4]Echeverria, T. 1981. Maturity in six species of rockfish (Pisces, Scorpaenidae, *Sebastes*). [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

[5]Echeverria, T. 1983. Maturity and seasonality of the rockfishes (Scorpaenidae: *Sebastes*) of central California. Unpubl. manuscr., 60 p. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

allows the use of standard least-squares regression techniques, and stabilizes variances (Bagenal 1978). Thus, rather than using ratios of fat or gonad volume to fish weight or length, which can be biased by allometric relationships between the measurements (Bagenal 1978; de Vlaming et al. 1982), we employed empirically derived regression lines. The use of power equations also allowed us to test hypotheses with standard statistical procedures. Regressions were calculated for each sex during each season. Although most of the analyses were for adults, seasonal regressions of visceral fat volume were also computed for juveniles when samples were large.

Differences between regressions of fat or gonad volume were tested by analysis of covariance, using the ratio:

$$F = \frac{(N - 4)(SS_{com.} - SS_1 - SS_2)}{2(SS_1 + SS_2)}$$

where SS_1 and SS_2 are the residual sums of squares about the separate regressions, $SS_{com.}$ is the residual sum of squares for a common regression, and N is the number of specimens (Kleinbaum and Kupper 1978). When regressions differed significantly, the direction of differences was assessed by examining the positions of the regression lines and of calculated volumes at mean fish length. We chose to display only the calculated volumes at mean length, to simplify the presentation of data. The mean of ln (total length) was determined for all specimens of a sex and species included in the annual analysis. For each season and sex, the estimated value of ln (volume) at the mean of ln (length) (designated $\hat{Y}$) was calculated from the appropriate regression. We intend these point values to be used only for making comparisons within our data. The regression lines themselves best represent fat or gonad volume, and we present the parameters for these regressions. See Guillemot (1982) for scatter diagrams of raw data and regression plots.

The estimated values of fat volume at mean length were also used in an index of the relative amplitude of fat cycles. This index was the antilog of the difference between estimated ln (fat volume) in peak and low seasons, and is equivalent to the ratio of peak season:low season fat volume.

We compared fat cycles of males and females within a species by qualitatively noting differences in the timing and amplitude of fat cycles, and by statistically comparing fat regressions during peak and low seasons of fat volume. The latter comparisons were carried out by analysis of covariance, as above.

In comparing fat cycles among species, we noted differences in the timing of fat cycles and differences in the amplitude of cycles. We also assessed differences in the absolute volume of fat stored by applying analyses of covariance to the peak-season fat regressions of the different species.

RESULTS

Seasonal Cycles of Fat and Gonad Volume in Adults

In most seasons, moderate to low correlations (0.5 and below) existed between ln (visceral fat volume) and ln (total length), indicating a fair amount of scatter about the regressions (Table 1). Lower correlations occurred mainly in seasons of low fat volume (cf. Fig. 1). The slopes of most regressions were not significantly different from 3.0 (Table 1), indicating a proportionate relationship between fat volume and fish length. Slopes significantly smaller than 3 occurred in seasons of low fat volume (winter and spring), and in general slopes from seasons of low fat volume were smaller than those from seasons of higher fat volume. During seasons of low fat volume, fish of all sizes tended to have little fat, accounting in part for some of the lower correlations. Some slopes were significantly greater than 3 during seasons of high fat content (*S. entomelas* females, *S. paucispinis* males, *S. pinniger* females, and *S. flavidus* females), indicating disproportionately greater fat content in larger fish. Correlations between ln (gonad volume) and ln (total length) were generally high (Table 2), and showed no marked relation with season (Fig. 2). Below, we first examine the fat and gonad cycles for adults of each species separately, and then briefly compare the cycles of different species.

Sebastes entomelas

Visceral fat content changed significantly during the year in both male and female *S. entomelas* (Fig. 1). In females, where all seasonal regressions of ln (visceral fat volume) on ln (total length) differed significantly from each other, fat content increased from a low in spring to a peak in fall, and then declined in winter (Fig. 1). In males, neither the spring and winter nor the summer and fall fat regressions differed significantly (Fig. 1). Visceral fat volume in males increased after spring to a peak spread through summer and fall, and then declined in winter (Fig. 1). During the fall, when both sexes had large volumes of visceral fat, fat content of males barely

TABLE 1.—Seasonal regressions of ln (visceral fat volume, ml) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California. Slopes significantly different from 3 are indicated (? = $P < 0.1$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Species and season	Females				Males			
	Sample size	Intercept	Slope	r	Sample size	Intercept	Slope	r
S. entomelas								
Spring	118	'21.752	3.845	0.240	88	– 12.267	2.341	0.138
Summer	102	– 23.875	4.335*	0.578	58	– 32.427	5.795?	0.456
Fall	81	– 28.715	5.184**	0.581	57	– 20.654	3.908	0.459
Winter	163	– 18.442	3.400	0.428	84	– 19.524	3.538	0.251
S. paucispinis								
Spring	117	– 10.334	1.988?	0.314	115	– 17.544	3.150	0.443
Summer	116	– 16.415	2.982	0.576	127	– 16.120	2.978	0.553
Fall	75	– 12.957	2.500	0.462	101	– 24.053	4.259**	0.693
Winter	82	– 1.269	0.633***	0.165	83	– 9.847	1.942*	0.389
S. goodei								
Spring	193	– 12.741	2.220	0.272	51	– 14.555	2.671	0.281
Summer	219	– 10.780	2.027	0.221	80	– 11.827	2.299	0.403
Fall	140	– 14.895	2.763	0.499	68	– 17.686	3.228	0.334
Winter	183	0.253	0.155***	0.020	55	0.783	– 0.026?	– 0.002
S. pinniger								
Spring	23	– 16.134	2.980	0.400	38	– 16.581	3.006	0.445
Summer	61	– 28.391	4.957***	0.786	103	– 17.213	3.152	0.455
Fall	32	– 24.771	4.453	0.579	37	– 14.859	2.825	0.593
Winter	18	– 24.371	4.289	0.529	14	– 28.849	5.063	0.538
S. flavidus								
Spring	73	8.221	– 1.038**	– 0.099	71	– 18.255	3.298	0.259
Summer	143	– 24.044	4.323**	0.605	88	– 10.960	2.152	0.240
Fall	147	– 14.050	2.771	0.468	112	– 8.652	1.777	0.212
Winter	69	– 2.946	0.743*	0.092	72	– 14.442	2.575	0.227

exceeded that of females. Fat regressions at the low point in spring did not differ significantly (Table 3).

As expected, gonad volume changed significantly during the year in both sexes of *S. entomelas* (Fig. 2). In males, the volume of testes increased dramatically from a low in spring to a peak in summer, and then declined through fall and winter (Fig. 2). In females, the volume of ovaries increased very slightly between spring and summer, and then increased greatly in fall and winter (Fig. 2).

Sebastes paucispinis

Visceral fat volume changed significantly during the year in males and females of *S. paucispinis* (Fig. 1). In females, fat content did not change significantly between spring and summer, but increased from summer to a peak in fall, to decline slightly in winter (Fig. 1). In males, visceral fat accumulated between spring and summer, remained about constant from summer to fall, and declined in winter (Fig. 1). During the nominal peak season in fall, fat content of females was significantly greater than that of males, while the regressions for fat content during the nominal low points in spring did not differ significantly (Table 3).

Ovarian volume in *S. paucispinis* reached its low point during summer, increased with vitellogenesis in fall, increased again with embryogenesis and/or further vitellogenesis in winter, and then declined in spring (Fig. 2). The volume of testes increased from spring into summer, continued to increase slightly in fall, and declined in winter (Fig. 2).

Sebastes goodei

Visceral fat volume in female *S. goodei* increased from spring through summer to a peak in fall, and declined in winter (Fig. 1). In male *S. goodei*, visceral fat volume increased from low levels in spring to a peak in summer, declined slightly in fall, and decreased again in winter (Fig. 1). The fat content of females during their fall peak exceeded that of males during their summer peak, while there was no significant difference in fat content during the low seasons of spring for females and winter for males (Table 3).

Ovarian volume increased slightly between spring and summer in females of *S. goodei*, and then grew more rapidly through fall and winter (Fig. 2). The volume of testes increased greatly between spring and summer in males of *S. goodei*, and then declined through fall and winter (Fig. 2).

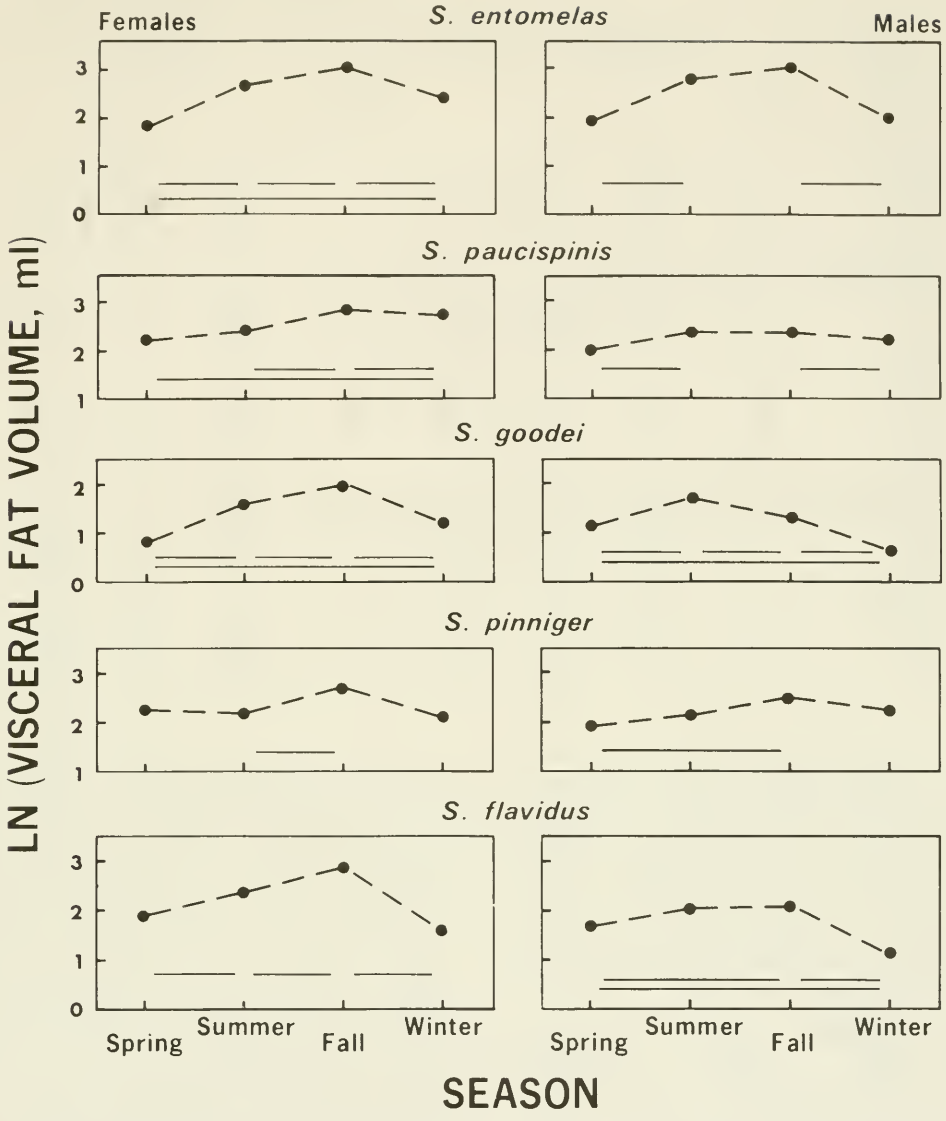

FIGURE 1. – Seasonal variation of visceral fat volume in adults of five species of *Sebastes* from northern and central California. For each species and sex, points are estimates of ln (fat volume) at the overall average of ln (total length) for specimens of that species and sex examined during the year. Estimates were derived from the seasonal regressions of ln (visceral fat volume) on ln (total length) (Table 1). A horizontal line between two seasons means that the fat regressions for those two seasons differed significantly ($P \leq 0.05$) by analysis of covariance. The upper of the two rows of horizontal lines are for adjacent seasons in the graph. The lower horizontal line is for winter and spring. The absence of a horizontal line means that the regressions did not differ significantly. Annual averages of ln (total length, mm) are *S. entomelas* females, 6.13, and males, 6.08; *S. paucispinis* females, 6.31, and males, 6.20; *S. goodei* females, 6.11, and males, 5.88; *S. pinniger* females, 6.11, and males, 6.14; and *S. flavidus* females, 6.11, and males, 6.04. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

TABLE 2.—Seasonal regressions of ln (gonad volume, mL) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California.

Species and season	Females				Males			
	Sample size	Intercept	Slope	r	Sample size	Intercept	Slope	r
S. entomelas								
Spring	217	−36.259	6.226	0.787	93	−40.725	6.738	0.709
Summer	17	−50.148	8.148	0.908	18	−42.341	7.386	0.644
Fall	65	−58.734	10.187	0.781	33	−10.442	1.930	0.191
Winter	177	−40.049	7.249	0.532	115	−18.856	3.207	0.403
S. paucispinis								
Spring	113	−26.341	4.541	0.640	163	−36.055	5.933	0.855
Summer	78	−34.265	5.767	0.919	105	−36.360	6.130	0.807
Fall	78	−37.533	6.386	0.833	118	−28.802	4.935	0.845
Winter	118	−34.058	5.946	0.647	127	−17.757	3.014	0.508
S. goodei								
Spring	146	−34.372	5.961	0.785	60	−20.612	3.552	0.332
Summer	166	−32.127	5.617	0.798	63	−12.733	2.386	0.283
Fall	176	−17.064	3.293	0.460	93	−29.433	5.095	0.772
Winter	184	−27.812	5.151	0.495	71	−17.172	2.886	0.214
S. pinniger								
Spring	21	−23.843	4.181	0.694	35	−49.963	8.230	0.799
Summer	22	−51.129	8.611	0.902	43	−60.352	10.175	0.939
Fall	31	−50.164	8.448	0.889	40	−45.336	7.564	0.845
Winter	21	−34.798	6.022	0.538	14	−65.227	10.657	0.904
S. flavidus								
Spring	100	−29.422	5.083	0.707	138	−31.837	5.228	0.499
Summer	83	−33.961	5.892	0.852	50	−54.152	9.204	0.759
Fall	162	−47.425	8.155	0.822	134	−38.906	6.649	0.690
Winter	53	−30.680	5.592	0.575	80	−23.743	3.927	0.555

TABLE 3.—Comparisons of fat volume between males and females during peak and low fat seasons in five species of *Sebastes*. If not defined statistically, peak and low seasons were selected on the basis of regression positions. $\hat{Y}$, the estimated ln (fat volume) at the overall average of ln (total length), is presented as an indication of regression position (Fig. 1). If male and female fat regressions differed significantly ($P \leq 0.05$) by analysis of covariance, their relative fat volumes are indicated. NS denotes regressions that did not differ significantly.

Species	Females		Males		Comparison
	Season	$\hat{Y}$	Season	$\hat{Y}$	
S. entomelas					
Peak	Fall	3.07	Fall	3.09	♂ > ♀
Low	Spring	1.82	Spring	1.96	NS
S. paucispinis					
Peak	Fall	2.81	Fall	2.35	♀ > ♂
Low	Spring	2.20	Spring	1.99	NS
S. goodei					
Peak	Fall	1.98	Summer	1.70	♀ > ♂
Low	Spring	0.82	Winter	0.63	NS
S. pinniger					
Peak	Fall	2.69	Fall	2.49	NS
S. flavidus					
Peak	Fall	2.87	Fall	2.08	♀ > ♂
Low	Winter	1.59	Winter	1.12	NS

Sebastes pinniger

Cycles of visceral fat volume were poorly defined in *S. pinniger*. In females, only the summer and fall fat regressions differed significantly, suggesting a peak in fat content during the fall (Fig. 1). In males, no two consecutive seasons differed significantly in fat content, and the only two seasons that differed significantly at all were spring and fall (Fig. 1). Thus, males may also have had peak fat content during fall, but their fat cycle was not pronounced. The visceral fat content of males and females did not differ significantly during their apparent fall peaks (Table 3).

The ovarian cycle of *S. pinniger* was also poorly defined in our data. Ovaries increased significantly in volume between spring and summer (Fig. 2). No other seasons differed significantly, but a peak in winter is indicated in Figure 2. In males, gonadal volume increased dramatically from spring to a peak in summer, remained fairly high in fall, and declined in winter (Fig. 2).

Sebastes flavidus

Visceral fat volume in female *S. flavidus* increased from spring through fall, and then declined in winter (Fig. 1). Male *S. flavidus* exhibited a gradual increase in fat content between spring and fall, followed by a decline to minimal fat levels in winter (Fig. 1). Fat content of females exceeded that of males during their fall peaks, and the difference in fat content during their winter lows was not significant (Table 3).

Ovarian volume in *S. flavidus* showed a pattern similar to most of the rest of the species: an increase

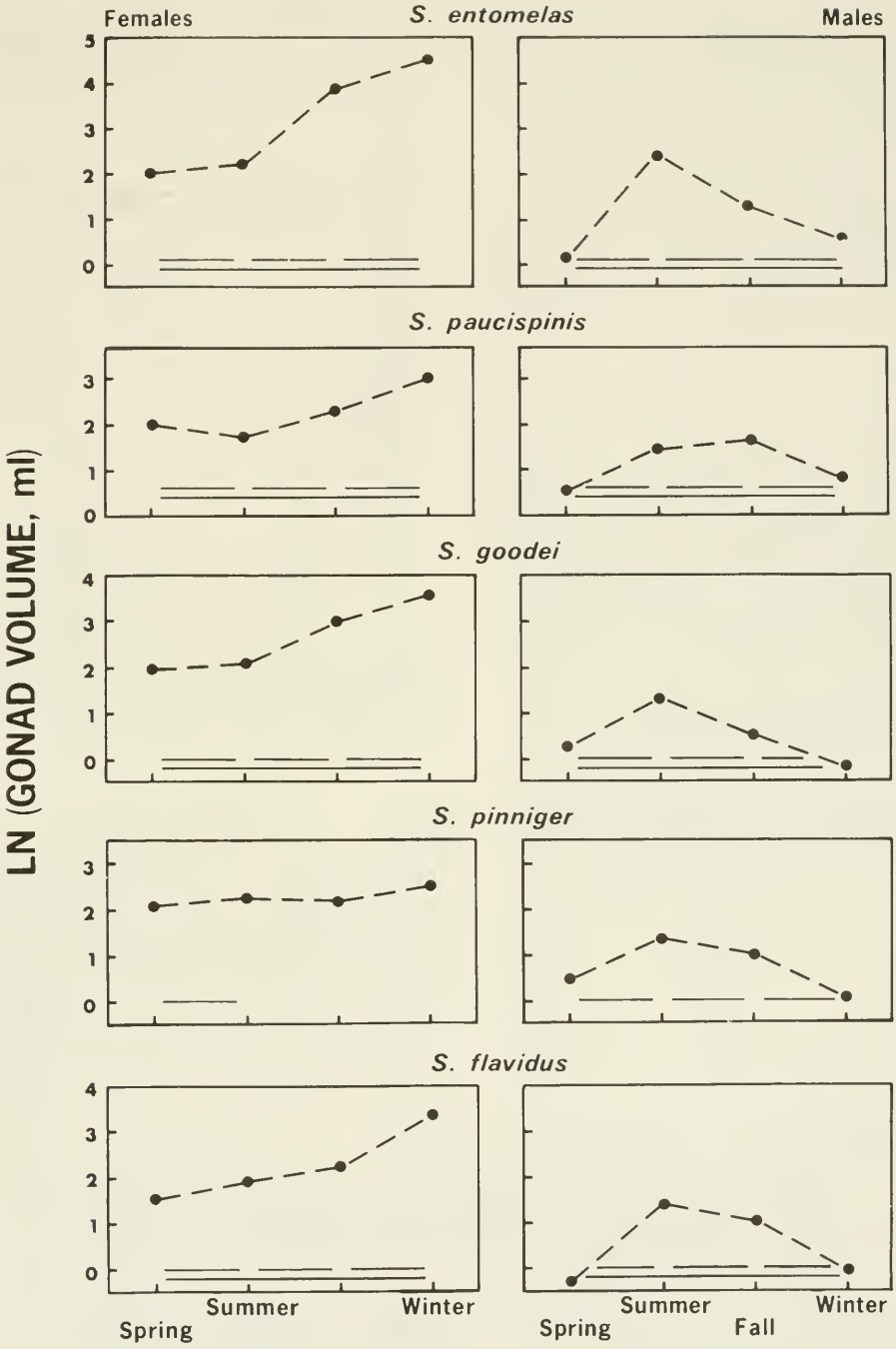

FIGURE 2.—Seasonal variation of gonad volume in adults of five species of *Sebastes* from northern and central California, as in Figure 1. Averages of ln (total length, mm) used in estimating gonadal volume are *S. entomelas* females, 6.14, and males, 6.06; *S. paucispinis* females, 6.24, and males, 6.17; *S. goodei* females, 6.09, and males, 5.88; *S. pinniger* females, 6.20, and males, 6.13; and *S. flavidus* females, 6.09, and males, 6.04. Seasons: spring (March-May 1981), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

from low volume in spring to peak volume in winter (Fig. 2). In males, the volume of testes increased from spring to a peak in summer, declined slightly in fall, and fell greatly in winter (Fig. 2).

Summary and Comparison of Adult Fat Cycles

In all species studied, visceral fat volume was high, if not at a peak, during fall. In males, fat content was usually high during summer as well. In male *S. entomelas*, *S. paucispinis*, and *S. flavidus*, summer and fall fat content did not differ significantly, and in male *S. goodei* the fat content in summer was actually greater than in fall. Summertime fat content was relatively high in female *S. entomelas*, *S. goodei*, and *S. flavidus*, but in females of all species the fat content increased to a peak in fall. Winter and spring were usually the seasons of low fat volume in both sexes. Little pattern existed in *S. pinniger*, except that fat volume appeared to reach a peak in fall.

Both the relative amplitude of fat cycles and peak fat volume differed among the species and sexes. In male and female *S. entomelas*, *S. goodei*, and *S. flavidus*, the fat volume of average-sized fish changed by about a factor of three during the year (Table 4). The amplitude of the fat cycle was lower in *S. paucispinis* and *S. pinniger*, where there was less than a twofold change in fat content between peak and low seasons (Table 4). Among females, *S. entomelas* and *S. flavidus* generally had higher peak fat volumes than the other species (Table 5). Among the other three species, peak fat content of females seemed to decrease from *S. pinniger* to *S. paucispinis* to *S. goodei* (Table 5). Females of *S. entomelas* and *S. flavidus*, then, possessed high-volume, high-amplitude fat cycles, while *S. pinniger* and *S. paucispinis* had low-volume, low-amplitude fat cycles, and *S. goodei* showed low volume and relatively high amplitude. The peak fat volume in male *S. entomelas* far exceeded that of the remaining species, most of which had relatively similar fat-length relationships during peak seasons (Table 5). Thus among males, only *S. entomelas* showed a high-volume, high-amplitude fat cycle. Males of *S. flavidus* and *S. goodei* possessed fat cycles of low volume and moderately high amplitude, and *S. paucispinis* and *S. pinniger* had cycles of low volume and low amplitude, like the females of these species.

TABLE 4.—Relative amplitude of fat cycles in five species of *Sebastes*. The ratio of estimated peak season: low season fat volume is presented for each species and sex, and is used as an index of cycle amplitude. Ratios are the antilogs of the differences between estimated ln (fat volume) at the average of ln (total length) in peak and low fat seasons (Fig. 1, Table 3).

	Amplitude	
Species	Females	Males
S. entomelas	3.50	3.10
S. paucispinis	1.83	1.44
S. goodei	3.20	2.91
S. pinniger	1.67	1.84
S. flavidus	3.61	2.64

Fat Cycles in Juveniles

Fat cycles were examined in juveniles of male and female *S. paucispinis*, and of female *S. pinniger* and *S. flavidus*, where seasonal sample sizes were large enough to permit analysis (Table 6). In *S. paucispinis*, juvenile females appeared to reach a peak in fat content during winter, but in juvenile males there were no significant differences among the seasonal regressions (Fig. 3). In *S. pinniger*, juvenile females

TABLE 5.—Comparisons of the peak-season regressions of ln (fat volume) on ln (total length) for different species of *Sebastes*. Comparisons were made by analysis of covariance. For significantly differing regressions ($P \leq 0.05$), the comparative fat volumes are indicated (based on the positions of the regressions, cf. Fig. 1, Table 1), unless intersecting lines made position difficult to interpret. NS denotes regressions that did not differ significantly.

	S. paucispinis	*S. goodei*	*S. pinniger*	*S. flavidus*
Females				
S. entomelas	*S.e.* > *S.pa.*	*S.e.* > *S.g.*	NS	NS
S. paucispinis		*S.pa.* > *S.g.*	NS	*S.pa.* < *S.f.*
S. goodei			*S.g.* < *S.pi.*	*S.g.* < *S.f.*
S. pinniger				*S.pi.* < *S.f.*
Males				
S. entomelas	*S.e.* > *S.pa.*	*S.e.* > *S.g.*	*S.e.* > *S.pi.*	*S.e.* > *S.f.*
S. paucispinis		intersection	*S.pa.* < *S.pi.*	intersection
S. goodei			NS	NS
S. pinniger				NS

possessed little fat in the spring, and higher levels in summer through winter (Fig. 3). Fat content in juveniles of female *S. flavidus* peaked in fall (Fig. 3).

TABLE 6.—Seasonal regressions of ln (visceral fat volume, mL) on ln (total length, mm) in juveniles of three species of *Sebastes* from northern and central California.

Species and sex	Season	Sample size	Intercept	Slope	r
S. paucispinis					
females	Spring	140	−19.637	3.510	0.325
	Summer	138	−26.793	4.669	0.455
	Fall	55	−23.626	4.189	0.419
	Winter	67	−29.508	5.205	0.719
males	Spring	92	−10.309	1.976	0.157
	Summer	86	−22.626	3.969	0.362
	Fall	10	−48.866	8.324	0.599
	Winter	21	−27.486	4.818	0.766
S. pinniger					
females	Spring	41	−21.012	3.655	0.402
	Summer	76	−21.794	3.859	0.624
	Fall	37	−36.539	6.383	0.875
	Winter	20	−18.568	3.345	0.651
S. flavidus					
females	Spring	21	−22.796	4.080	0.388
	Summer	70	−8.502	1.642	0.260
	Fall	53	−36.450	6.558	0.639
	Winter	19	−9.906	1.848	0.361

Thus, in three of the four groups analyzed, fat content of juveniles varied during the year. The timing of the apparent cycles was similar to that of adults. The amplitude of the fat cycle in juveniles of female *S. paucispinis* and *S. pinniger* (less than twofold change in fat volume) was similar to adult amplitude. In female *S. flavidus*, the amplitude of the fat cycle in juveniles (less than twofold change) was lower than in adults. As adults, *S. flavidus* showed high-amplitude fat cycles, while *S. paucispinis* and *S. pinniger* showed low-amplitude cycles.

DISCUSSION

Clear cycles of visceral fat volume and gonadal volume occurred in both sexes of *S. entomelas*, *S. paucispinis*, *S. goodei*, and *S. flavidus*. The fat cycles of male and female *S. pinniger* were less well-defined, as was the gonadal cycle of female *S. pinniger*. Many of the female *S. pinniger* we examined were relatively small adults. This may account, at least in part, for the small and ill-defined fat and gonad cycles, as the fat cycles of female *S. flavidus* increased in amplitude from juveniles to adults.

Visceral fat volume generally increased propor-

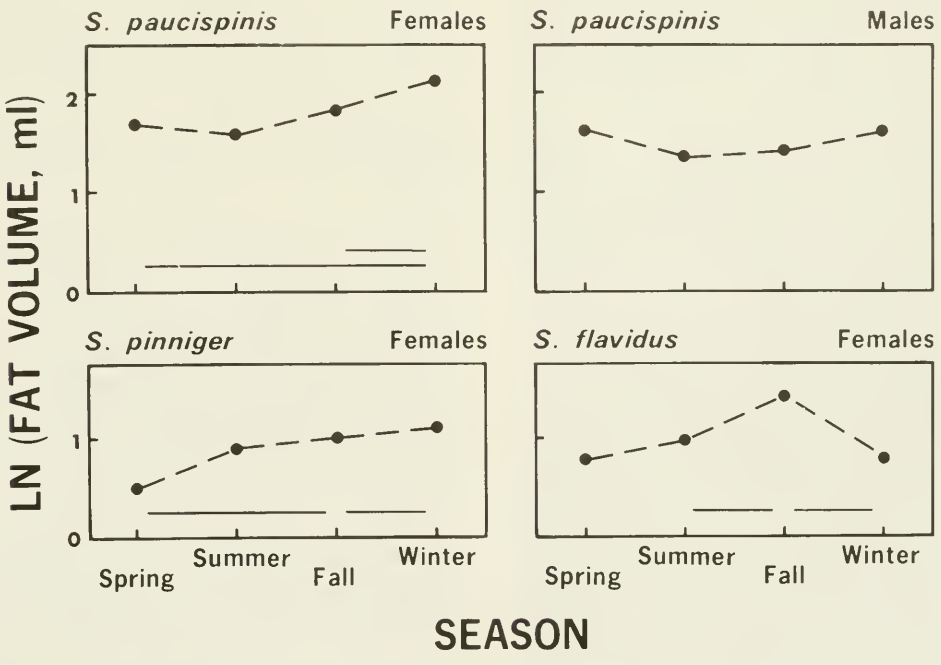

FIGURE 3.—Seasonal variation of visceral fat volume in the juveniles of five species of *Sebastes*, as in Figure 1. Averages of ln (total length, mm) used in estimating fat volume are *S. paucispinis* females, 6.08, and males, 6.04; *S. pinniger* females, 5.88; and *S. flavidus* females, 5.78. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

tionately with fish volume, since most slopes of ln (fat volume) on ln (length) were near 3. Slopes smaller than 3 occurred in those seasons when fish of all sizes had little fat. Some slopes during seasons of high fat volume were significantly greater than 3, indicating that larger fish had disproportionately greater fat volume than smaller fish. This was particularly true of, but not limited to, the species and sexes with high-magnitude fat cycles (males and females of *S. entomelas* and females of *S. flavidus*). It would be interesting to discover whether larger females of *S. pinniger* have high-amplitude fat cycles, since the slopes of the fat regressions for female *S. pinniger* were relatively high.

The dependence of fat volume on fish size and season of collection, while applicable on average, does not apply to every individual. The scatter about the regressions of fat volume on length was large. Some of the scatter was probably due to errors in measurement, but a large part was real. We have observed large differences in the amount of visceral fat among fish of the same size and sex in the same collection. The reasons for such variation may be difficult to resolve, since it is difficult to know the history of individuals collected in the field.

However, our data were adequate in most species to detect seasonal changes on average. We wanted to compare the timing of fat cycles and gonad cycles, and thus learn something of the function of fat storage in rockfish. Our initial hypothesis was that stored fat would be used in reproduction, based on Roberts' (1979) observations.

The data for males do not support this hypothesis. Fat and gonad cycles were nearly coincident, with peaks in both cycles occurring in fall and/or summer and lows in winter/spring. Thus the energy for gonadal growth was probably derived from current ingestion, not from material previously stored as fat. Maximum somatic growth also coincides with the summertime growth of testes and fat deposits (e.g., Love and Westphal 1981), so all three processes may be competing for energy consumed during this time.

The situation is more complicated in females. Some fat was deposited between spring and summer in females of *S. entomelas*, *S. goodei*, and *S. flavidus*, and females of all species gained fat between summer and fall. Some gonadal growth took place between spring and summer in females of all species except *S. paucispinis*. In all but *S. pinniger*, however, ovarian volume increased steadily between summer and winter. The growth of ovaries through fall was due largely to vitellogenesis, while the greater growth of ovaries into winter was due primarily to embryogenesis and hydration of ova (Moser 1967). Additional vitellogenesis probably occurred during winter in the multiple spawners, *S. paucispinis* and *S. goodei* (Moser 1967; MacGregor 1970).

In females, then, fat deposition usually began in summer, perhaps slightly before the initiation of vitellogenesis, but continued into the main period of vitellogenesis between summer and fall. Thus, like males, females of these species deposited fat more or less concurrently with gonadal maturation and somatic growth. The depletion of visceral fats occurred between fall and spring in females of most species, during and after gestation. It is possible that fat reserves are used for the maturation of additional ova in multiple spawners or are involved in the nutrition of embryos (Boehlert and Yoklavich 1984), but as in males, reserves are not used in the initial development of gonads.

There were two main differences in the fat cycles of males and females: females usually had larger fat cycles than males, and the peak fat volume of females occurred in fall, while fat volume in males usually reached a plateau that spread through summer and fall. It is possible that courtship activity in males (Helvey 1982) draws energy from fat deposition between summer and fall, or that this activity draws time from feeding. As a result, females may continue to fatten after fat deposition ceases in males. It is also possible that females require more reserves in winter and they somehow are able to acquire these extra reserves.

The synchronous depletion of reserves in males and females, however, indicates a common function for such reserves. We suggest two possible functions:

First, some rockfish may migrate during the period of fat depletion. Love (1981) presented evidence for seasonal movements in *Sebastes paucispinis* and *S. entomelas* off southern California, but had no data on the extent or direction of movement. Females of *S. alutus* undertake seasonal migrations covering as much as 300 m of depth (summarized in Gunderson 1977). Lenarz (pers. obs.) found evidence of seasonal movement in female *S. jordani*. Several species of rockfish undertake little or no seasonal migration, including *S. flavidus* from shallow waters off Alaska (Carlson and Barr 1977). Since seasonal migrations in rockfish may not be long and seem to occur primarily in females, we suggest that other possibilities be ruled out before accepting migration as a major use of fat reserves.

Second, we suggest that fat reserves are used for maintenance during wintertime periods of reduced food availability. Fattening, as well as growth and

initial gametogenesis, occurs during and shortly after the spring-summer upwelling period, and depletion occurs during and after a time of lower primary production (Bolin and Abbott 1963). Roberts (1979) noted that several species of inshore rockfish near Monterey consumed more food during the summer, when macroplankton (euphausiids) and juvenile rockfish were abundant. During the nonupwelling season, juvenile rockfish and macroplankton were less abundant, and adult rockfish consumed less food. Love and Westphal (1981) found less food in the stomachs of *S. serranoides* during the nonupwelling season near Morro Bay. Gunderson (1977) noted a "summer feeding season" in *S. alutus*. Hobson and Chess[7], however, found the gelatinous prey of *S. mystinus* to be more abundant during nonupwelling periods off northern California. There is only limited information on the seasonal food habits of the five species studied here. *Sebastes paucispinis* is largely piscivorous (Phillips 1964), while *S. entomelas*, *S. goodei*, *S. pinniger*, and *S. flavidus* feed on macroplankton and small fish (Phillips 1964; Pereyra et al. 1969; Brodeur 1982). Brodeur (1982) examined seasonal changes in the diets of *S. flavidus* and *S. pinniger*, and found that food consumption declined during winter in *S. pinniger*, but not in *S. flavidus*. However, Carlson and Barr (1977) found a pronounced decline in activity during winter in *S. flavidus* off Alaska, suggesting seasonal changes in feeding. This hypothesis can be examined with concurrent data on food consumption and fat volume. It is not mutually exclusive with other functions of fat reserves, since some fat could also be used for migration, nourishment of embryos, or maturation of additional ova in multiple spawners.

The wintertime use of reserves for maintenance, however, is consistent with the overall pattern of long life and repeated reproduction in rockfish (as discussed also by Gunderson [1977]). As suggested by Slobodkin (1962) and Calow (1977), summertime fat deposition may exact a cost in current reproduction (if more gametes could be packed into rockfish abdomens) or in future increases in gamete capacity (through additional growth), but may help to ensure survival.

An interesting result of our study was the difference in magnitude of fat cycles among species, which was particularly evident in females. These differences are correlated with both the frequency of spawning and geographical distributions of the species. Females of *S. entomelas* and *S. flavidus* had fat cycles of high amplitude and volume, probably spawn only once a year (Westrheim 1975; Echeverria footnote 5), and have northerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). On the other hand, *S. paucispinis* and *S. goodei* had fat cycles of low amplitude and/or volume, spawn more than once a season, at least in southern California, and have southerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). The case with *S. pinniger* is unclear. Females seemed to have low-amplitude fat cycles, but the small sample and small sizes of females in the samples make conclusions tenuous. Echeverria (footnote 5) has some evidence for multiple spawning in *S. pinniger*. If so, its northerly distribution would be inconsistent with the pattern seen in the other species. We will restrict our discussion to the remaining four species, although further studies of *S. pinniger* may be instrumental in evaluating the suggestions we make below.

The small fat cycles of multiple spawners are probably not caused by their potentially greater reproductive output, since fat deposition stops long before the maturation of additional batches of ova. It seems more likely that the magnitude of the fat cycle, frequency of spawning, and geographical distribution are all related. Boehlert and Kappenman (1980) suggested that year-round spawning in southern populations of *S. diploproa* served to increase reproductive output in response to annual variation in the survival of planktonic larvae. Multiple spawning in southern populations and species may also be a response to the more even seasonal distribution of upwelling in southern vs. northern areas of the northeastern Pacific (Bakun et al. 1974; Parrish et al. 1981; Smith 1978), as it affects planktonic larvae. However, the more restricted upwelling season in northern waters may also lead to larger and better defined seasonal variation in the food supply of adults. A more pronounced summertime pulse of food may enable northerly species like *S. entomelas* and *S. flavidus* to store large amounts of fat. Similarly, a more pronounced decline in food during winter may make the accumulation of such reserves necessary, and preclude the maturation of additional batches of ova. On the other hand, a more even seasonal distribution of food in the south may enable southerly species like *S. paucispinis* and *S. goodei* to produce additional batches of ova during winter, and may also reduce the need for wintertime reserves. These suggestions are speculative, but it should be possible to compare the seasonal variation of food consumption in species with northern vs. southern distributions.

[7]Hobson, E. S., and J. R. Chess. 1981. Seasonal patterns in trophic relationships of the blue rockfish, *Sebastes mystinus*. [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

In summary, we suggest that seasonal changes in the availability of food are rather important in the life histories of rockfish. The summer storage and winter use of fat reserves, in near synchrony with growth and decline of gonad volume, indicate a wintertime paucity of food that is compensated by the use of material that was stored at the expense of fecundity or growth. Further study of seasonal feeding, fat deposition, and reproductive cycles, categorized by size and sex, would be useful in evaluating this hypothesis. Further, geographical comparisons of these cycles may illuminate some causes of differences in the life histories of rockfishes.

ACKNOWLEDGMENTS

For their assistance during the course of the study, we thank Tina Echeverria, Pete Adams, Connie Ryan, Nancy Wiley, and many other employees of NMFS and the California Department of Fish and Game. Pete Adams, Tom Niesen, and George Boehlert suggested improvements in the manuscript. Diane Fenster drafted the figures. This paper is derived from the senior author's Master's thesis at San Francisco State University. The work took place at the Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, CA, under a NMFS student appointment.

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THE POSSIBLE INFLUENCE OF WARM CORE GULF STREAM RINGS UPON SHELF WATER LARVAL FISH DISTRIBUTION

G. R. FLIERL[1] AND J. S. WROBLEWSKI[2]

ABSTRACT

We propose a simple one-dimensional model for examining the impact of warm core rings upon the larval fish distribution and abundance over the continental shelf off the northeastern United States. The model includes (in a cross-shelf averaged sense) the loss of larvae due to biological causes of mortality, the advective transport of larvae due to the mean down-shelf currents, and the changes in larval density produced by the on-shelf or off-shelf flows occurring when a ring approaches the shelf-slope front. The results of this highly idealized model indicate that the decreases in larval abundance caused by cross-shelf flows may be as large as those caused by biological factors and, furthermore, the effects are strongly dependent upon the rate of motion of the ring. A stationary ring may cause a 20 to 50% drop in abundance, depending on the strength and size of the ring and on the longshore velocity in the shelf water. When the ring is slowly moving, the impact can be even greater: a patch of larvae being advected downshelf by the longshore current could, when catching up to the back side of an eddy, essentially be swept off the shelf, decimating the patch.

Model predictions are compared with historical MARMAP data of larval cod and haddock density in the Georges Bank area. There does appear to be a relationship between the frequency of ring interaction with Georges Bank and the subsequent year-class strength of cod and haddock stocks. Thus we suggest that further investigation of the impacts of rings is warranted, both from the observational and the theoretical viewpoints. These studies should include detailed measurements in entrainment features, further analysis of ring-Bank interactions factoring in the closeness of the ring, the strength of its currents and its translation rate, and more detailed modelling of entrainment events and larval fish ecology.

Warm core rings form in the Slope Water region between the North American continental shelf and the Gulf Stream. These rings are eddies 100 to 200 km in diameter which result when a Gulf Stream meander separates from the main current. The potential impact of warm core rings upon the continental shelf ecosystem has become more apparent with routine satellite infrared images of the sea surface. Charts of sea surface temperature prepared from these images, e.g., Figure 1, (Halliwell and Mooers 1979; Chamberlin 1981) frequently show rings entraining cold water from the continental shelf. This interpretation is supported by ship observations and current meter records of water transport onto and off the continental shelf induced by warm core rings (Morgan and Bishop 1977; Smith 1978; Smith and Petrie 1982). Physical and biological oceanographers have long been aware of occasional intrusions of anomalously warm water onto Georges Bank (for a review, see Bolz and Lough 1981), which are now likely to be attributable to warm core ring activity. In 1961 Colton and Temple hypothesized that large numbers of larval fish of shelf species can be drawn off Georges Bank into warmer Slope Water where they succumb to unfavorable environmental conditions (c.f. Laurence and Rogers 1976).

The purpose of this paper is to examine theoretically the possible influence of warm core rings on the abundance and distribution of larval fish in continental shelf waters off the northeastern United States, in particular the shelf region associated with cod and haddock spawning on Georges Bank. Our study makes estimates of the advective losses of larvae because of the entrainment of shelf water by an eddy and predicts changes in larval density (the observable quantity in ichthyoplankton surveys) because of the onshore and offshore flows induced by a ring. We also consider the possible biological causes of mortality (e.g., predation, physiological death). In other words we wish to estimate the relative importance of the physical and biological losses via a mathematical model. While our model does not describe either in great detail, we feel that it does indicate the importance of ring-induced entrainment and the dependence of this effect upon the speed of translation of the ring, the width over which it interacts with the shelf, and the strength of its currents at the shelf break. We compare our model predictions of the spatial and temporal distributions of larval fish

[1]Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139.
[2]Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada; present address: Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME 04575.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

with the historical MARMAP (Maritime Resources Monitoring, Assessment and Prediction) data of larval cod and haddock distributions in the Georges Bank area (Smith et al. 1979). We also present an apparent relationship between years of low warm core ring activity and strong year classes in the fishery.

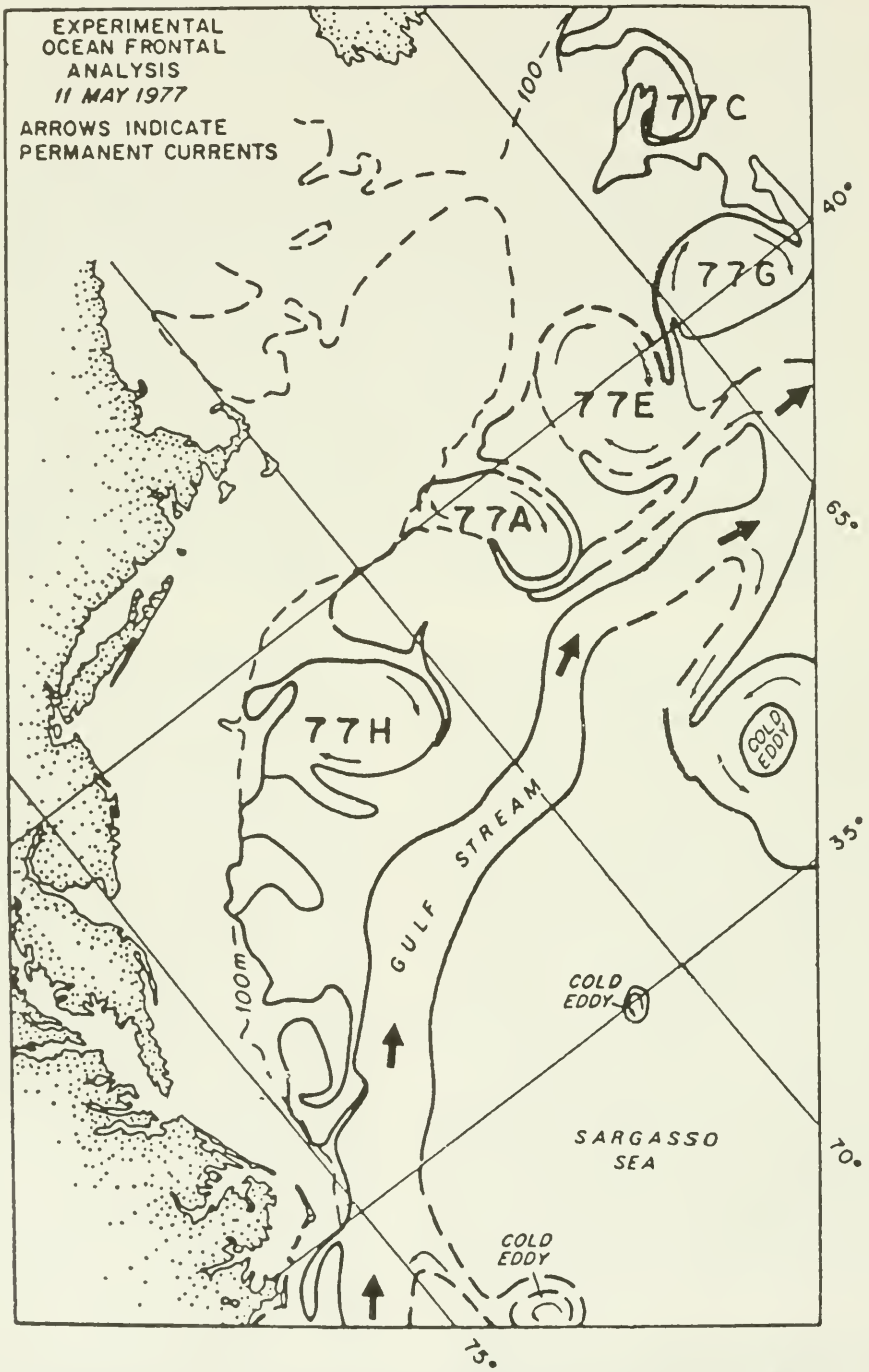

FIGURE 1.—Distribution of warm core rings off the U.S. northeast coast during the week of 11 May 1977. The chart was produced by the U.S. Naval Oceanographic Office from infrared satellite images.

Finally, we make recommendations for further investigations of the influence of warm core rings on the northeast coast marine ecosystem.

Our very simplified modelling approach to the problem of resolving biological distributions in a variable oceanic flow regime could, with proper reparameterizations, be applied to estimating the impact of rings on chemical distributions as well—an example would be determining the distribution of pollutants dumped in deepwater dumpsite 106. For variables which do not behave as passive particles in the flow, the model has limitations. Vertical migration behavior by fish larvae may play an important role in their distribution which is not resolved by our preliminary modelling. Other potentially important details, such as the mechanism for mixing on the shelf, have also not been included in this first, simplified calculation. Nevertheless, we feel that the results are extremely suggestive, indicating ways to examine existing data sets and hypotheses to be tested in future field studies.

THE MODEL

There are many possible approaches to modelling the effects of rings upon fish larvae, ranging from simple order-of-magnitude estimates to complex physical models which predict the mean and varying currents from winds, heating, topography, and coastlines. The water motions could then be coupled with complex biological models of spawning, predation, growth, and mortality. However, we are not yet at the stage where such a full-scale calculation is really justifiable; we do not understand enough about the physics of the shelf-slope region and the rings or enough about larval fish biology to ensure that only important processes are included and that these are being properly represented in our numerical model. In addition, the questions we wish to address are fairly simple ones: How large could the impact of rings upon larval fish populations be and how do these impacts depend upon the flow structure and translational speed of the rings? We, therefore, shall take the simplest approach to the problem of estimating our primary variable, the larval fish density (or abundance). The various processes which affect the population distribution will be represented in the model in an almost schematic form. The actual populations vary in all three dimensions and in time, but we shall include only the downstream and time variations in the model. Likewise, the actual current patterns are quite complicated and we choose only to represent the impact of the ring-induced currents by a specification of the flow at the outer edge of the shelf, with onshore flow ahead of the ring and offshore flow behind the eddy. The mean downshelf drift currents will also be included. The biological processes of predation, physiological mortality, and metamorphosis out of the planktonic larval stage will be represented simply as a loss rate μ which will be assumed to be independent of space or time. With these simplifications, the general equation governing the density $n(x,y,z,t)$ of the planktonic larvae can be reduced to a manageable form

$$\frac{\partial}{\partial t} n + \frac{\partial}{\partial x} un + \frac{\partial}{\partial y} vn + \frac{\partial}{\partial z} wn = -\mu n. \qquad (1)$$

We shall use the geometry shown in Figure 2 with x the downshelf coordinate, y the offshore coordinate,

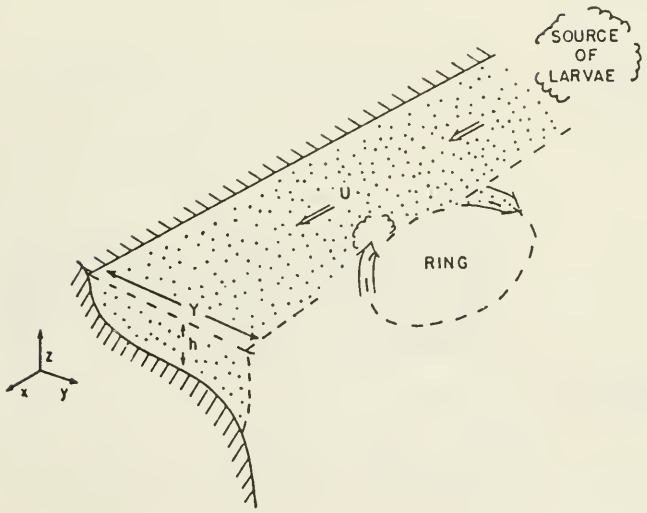

FIGURE 2.—Schematic diagram of the geometry assumed in the mathematical model. Y is the shelf width, h is the average depth, and U is the average longshore velocity of the shelf water.

and z positive upwards. We shall assume that there is a source of larvae somewhere upstream of $x = 0$, e.g., the spawning grounds on Georges Bank, leading to a specified flux of organisms into the domain at the $x = 0$ boundary. Alternatively, and more conveniently, the upstream spawning can be thought of as leading to a specified abundance of organisms $N_0(t)$ at $x = 0$.

Although we could, in principle, specify the three-dimensional currents and the source function N_0 from either measurements or models, the available data and models are not really adequate for this to be possible. We have chosen, therefore, to simplify the model further by averaging the larval fish density vertically and across the shelf

$$N(x,t) = \frac{1}{hY}\int_0^Y \int_{-h}^0 n(x,y,z,t)\, dz\, dy. \tag{2}$$

Here Y is the width of the shelf and h is the depth (both assumed independent of x). We can find the equation governing this N by averaging Equation (1) over the shelf width and depth, applying boundary conditions of zero flux through the upper and lower surfaces and the continent side of the domain. This gives

$$\frac{\partial}{\partial t}N + \frac{\partial}{\partial x}\left[\frac{1}{hY}\int_0^Y \int_{-h}^0 un\, dz\, dy\right] + \frac{1}{hY}\int_{-h}^0 v(x,Y,z,t)\, n(x,Y,z,t)\, dz = -\mu N. \tag{3}$$

The downstream variation of Y and h has been neglected although it is not too difficult to include it. The term representing downstream advection of larvae will be simplified by assuming that the cross-shelf mixing of larvae is sufficiently intense that n is uniform in y. The along-shelf advection term then becomes

$$\frac{\partial}{\partial x}\frac{1}{hY}\int_0^Y \int_{-h}^0 un\, dz\, dy \cong \frac{\partial}{\partial x}UN;$$

$$U(x,t) = \frac{1}{hY}\int_0^Y \int_{-h}^0 u(x,y,z,t)\, dz\, dy. \tag{4}$$

Similarly, we shall ignore vertical variations in n at the shelf edge so that the flux off the shelf becomes

$$\frac{1}{hY}\int_{-h}^0 v(x,Y,z,t)\, n(x,Y,z,t)\, dz \cong \frac{N_e V_0}{Y};$$

$$V_0(x,t) = \frac{1}{h}\int_{-h}^0 v(x,Y,z,t)\, dz. \tag{5}$$

Here $V_0(x,t)$ is the depth-averaged onshore-offshore flow (positive offshore) and N_e is the depth-averaged larval fish density in the water which is moving onto or off of the shelf. (Vertical migratory behavior which is somehow correlated with vertical shears would alter this parameterization of the outflowing flux of larvae.)

When there is onshore or offshore flow, the averaged velocity along the shelf cannot be constant. The variations in U can be calculated from the conservation of fluid volume integrated across the shelf

$$\frac{\partial}{\partial x}\left[\frac{1}{hY}\int_0^Y \int_{-h}^0 u\, dz\, dy\right] + \frac{V_0}{Y} = 0$$

$$\text{which implies } \frac{\partial U}{\partial x} = -\frac{V_0}{Y}. \tag{6}$$

Finally we must introduce a parameterization for the density of larvae carried on or off the shelf at the edge N_e in terms of the average density $N(x,t)$. It is assumed that the Slope Water pushed onto the shelf by the ring is devoid of shelf fish larvae. If we presume that this Slope Water mixes completely with the shelf water, then the water leaving the shelf carries larvae with density N, as sketched in Figure 2. These considerations suggest that the entrainment term can be modelled by

$$N_e = \begin{cases} 0 & \text{for } V_0 < 0 \\ N & \text{for } V_0 > 0 \end{cases}. \tag{7}$$

(Again, we must remark upon the limitations of the present calculation; certainly the shelf water is not thoroughly mixed and the density of the outflowing larvae is much more complicated and perhaps smaller on the whole than this formula would suggest. We hope that our results will spur further modelling and observational efforts to assess the processes we have been forced to represent so crudely.) When all of these simplifications are gathered together, the approximate equations for the average density of larvae $N(x,t)$ become

$$\frac{\partial}{\partial t}N + \frac{\partial}{\partial x}(UN) + \begin{cases} 0 & \text{for } V_0 < 0 \\ \dfrac{V_0 N}{Y} & \text{for } V_0 > 0 \end{cases} = -\mu N$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y} \tag{8}$$

with the boundary condition

$$N(0,t) = N_0(t). \tag{9}$$

STATIONARY EDDIES

In nature, there are pulses of larvae entering the domain as the fish spawn. In addition, the shelf-edge velocities $V_0(x,t)$ are changing as mesoscale eddies and Gulf Stream warm core rings impinge upon the shelf. We shall present in the section on moving eddies several numerical solutions of Equations (8) and (9), simulating this complex situation. However, in order to fully understand the importance of the rings and eddies in determining the fish larvae's spatial distribution, it is first useful to consider some simpler, analytically tractable cases. We shall begin by discussing the distributions which occur when the shelf-edge flows are not changing with time, i.e., the eddies are stationary. This problem also has bearing on the real situation south of Long Island, where rings may often stop for considerable lengths of time.

As a first example, consider the larval fish distribution which would occur in the absence of any biological loss processes ($\mu = 0$) and when the source term N_0 is independent of time. The resulting equations

$$\frac{\partial}{\partial x}(UN) = \begin{cases} -V_0 \dfrac{N}{Y} & \text{for } V_0 > 0 \\ 0 & \text{for } V_0 < 0 \end{cases},$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y} \tag{10}$$

can be solved readily

$$N = \begin{cases} N_0 \dfrac{U_0}{U} = \dfrac{N_0 U_0}{U_0 - \displaystyle\int_0^x \frac{V_0}{Y}} & \text{if } V_0 < 0 \qquad (11a) \\ N_0 & \text{if } V_0 > 0 \text{ and } U_0 > \displaystyle\int_0^x \frac{V_0}{Y} \qquad (11b) \\ 0 & \text{if } V_0 > 0 \text{ and } U_0 < \displaystyle\int_0^x \frac{V_0}{Y} \qquad (11c) \end{cases}$$

where U_0 is the longshore velocity and N_0 is the (time-independent) population density at the upstream boundary $x = 0$. We can now see explicitly the effects of the physics alone upon the larval fish distribution. In the regions where the flow is onto the shelf (Equation (11a)), the shelf break boundary contribution to Equation (10) is zero. But the effects of the flow field are still felt in that the along-shelf flow is divergent. U increases downstream as water comes onto the shelf, spreading out the larvae and reducing their average density. In contrast, when the flow is offshore (Equations (11b) or (11c)), there are direct loss terms due to larvae being carried off the shelf. Some of the water flowing into a section are diverted offshore while some continues down the shelf, with the larvae separating in the same proportions. Thus, although there is a decreased flux down the shelf, this does not affect the density since there are no biological losses which need to be balanced by this flux. The net effect is that the physics by itself does not change the population density in regions of offshore flow (Equation (11b)). The only exception would occur when the offshore transport ($\int V_0\, dx$) is sufficiently strong so that all of the normal alongshore flow ($U_0\, Y$) is diverted off the shelf. In this case (Equation (11c)), the flow in regions farther down the shelf is reversed and the water moves up the shelf. Since this water is from regions without sources of larvae, the population density is zero.

By putting together these two results, we can construct a picture of the density of larvae in continental shelf water flowing past a stationary ring centered at $x = D$. This is shown in Figure 3. For these calculations we have used

$$V_0 = -A \frac{x - D}{L} \exp\left[\frac{1}{2} - \frac{1}{2}\frac{(x-D)^2}{L^2}\right] \tag{12}$$

with $A = 20$ cm/s the peak offshore velocity) and $L = 20$ km (so that roughly 80 km along the shelf is strongly influenced by the ring currents). This figure

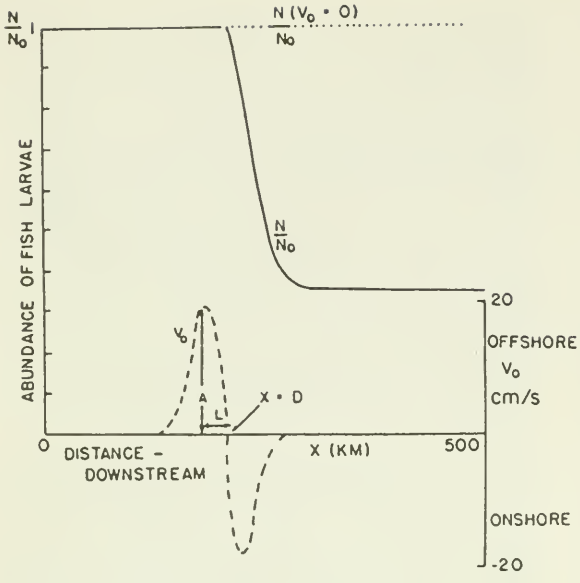

FIGURE 3.—The steady state abundance of fish larvae with distance along the shelf. This abundance is expressed as a fraction of the number of larvae continuously being produced at the spawning site, N_0. There is a 80 km wide, stationary eddy at the shelf edge, inducing onshore and offshore flows of 20 cm/s. The longshore velocity U_0 of the shelf water is 5 cm/s. Biological losses (μ) are set equal to zero. The dotted line shows the steady abundance of fish larvae with distance down the shelf when there is no eddy present.

shows only the spatial distribution of larval density in the water moving down the shelf, as affected by flow convergences or divergences associated with the physics of the ring. The flux of larvae off the shelf (not shown) is given by $V_0\, hN_0$ in the regions where V_0 is greater than zero and amounts in total to

$$\int_0^D V_0\, h\, N_0\, dx \cong A\, h\, L\, N_0\, e^{1/2}.$$

66% of the flux into the domain ($U_0\, N_0\, hY$) at $x = 0$. Next, we shall see that the physics and biology actually interact to produce a greater net impact than when either is considered separately.

For this second model problem, we shall still use a steady onshore and offshore flow pattern, but now include the biological loss term and the time-dependence in the source function N_0. When the flow is offshore or zero, the population distribution is given by

$$N(x,t) = N_0(t - \tau)\, e^{-\mu\tau} \tag{13a}$$

where the variable τ measures the length of time necessary to reach the point x from the upstream edge of the domain. In general τ is given by

$$\tau = \int_0^x \frac{dx}{U(x')} \tag{13b}$$

where $U(x)$ can be found by integrating the mass conservation equation

$$U(x) = U_0 - \int_0^x dx' \frac{V_0(x')}{Y}. \tag{13c}$$

In the absence of ring-induced onshore-offshore flows ($V_0 = 0$), however, τ is just equal to x/U_0 and

$$N(x,t) = N_0 \left(t - \frac{x}{U_0}\right) e^{-\mu x/U_0}. \tag{13d}$$

The population at any downstream point lags that at the origin by the travel time x/U_0 and has also decayed exponentially during its travel. This solution is an important base case for understanding the distributions in a spawned patch which has not been impacted by rings.

When water is being drawn off the shelf, the alongshelf decay in concentration is again purely due to travel time, since the effect of losses off the shelf on the density is compensated for by the convergence. However the spatial density of the larvae is still noticeably altered by the offshore flow because the travel time necessary to reach any point is increased. This occurs because U is decreasing with x as a result of the advection of water off the shelf (as shown in Equation (13c)). Since U is less than U_0, the travel time τ in Equation (13b) is necessarily greater than that in the absence of the ring (x/U_0). We have sketched $\tau(x)$ for the three possible signs of V_0 in Figure 4a. These results suggest that there will be an enhanced spatial decay rate of larval density in the regions where the flow is offshore.

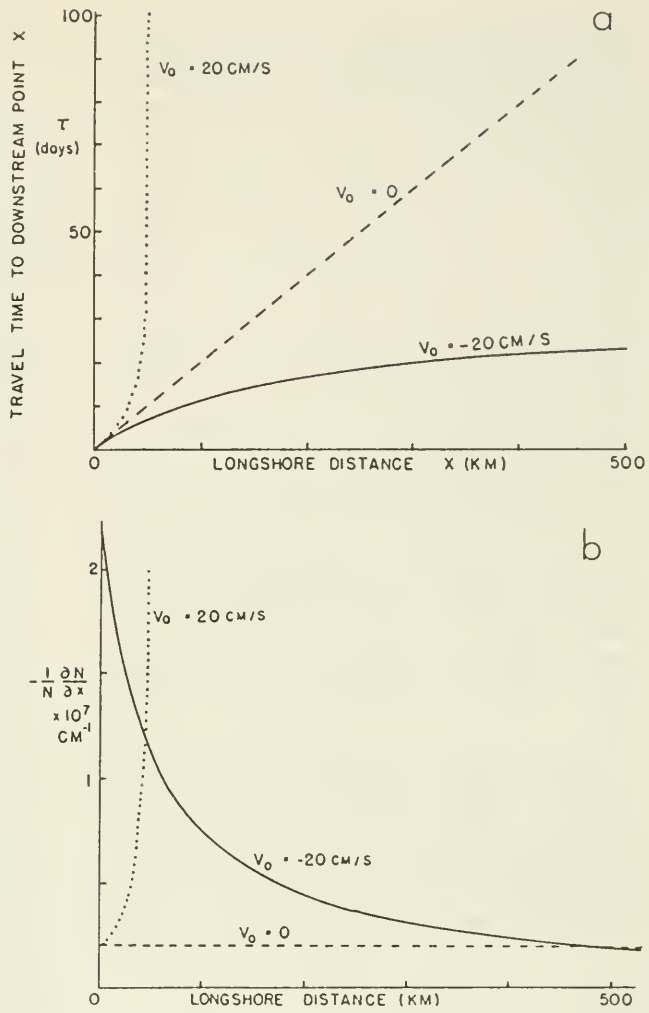

FIGURE 4.—a) The travel time τ necessary for larvae to reach the point x down the shelf from the spawning site at x = 0. The values of τ are computed in the absence of an eddy ($V_0 = 0$) and when an eddy induces onshore ($V_0 = -20$ cm/s) and offshore ($V_0 = 20$ cm/s) flows. b) The rate of change in numbers of larvae N with distance down the shelf x, plotted against longshore position for the three values of V_0.

When the flow is onshore ($V_0 < 0$) we can also solve Equations (8) and (9) and find

$$N(x,t) = N_0(t - \tau)\,\frac{U_0}{U(x)}\,e^{-\mu\tau}. \tag{14}$$

In this case, the timelike variable τ increases less rapidly with x than in the base case. This alone would lead to a slower spatial decay; however, the dilution effect (the U_0/U factor) counters this. In most cases, the dilution will be stronger than the effects of decreased transit time.

Perhaps the simplest way to see this is to consider the downstream decay rates when the source of larvae is constant in time and the onshore or offshore flows are spatially uniform. The spatial decay rates $-(\partial N/\partial x)/N$ for the three flow cases are

$$-\frac{1}{N}\frac{\partial N}{\partial x} = \begin{cases} \dfrac{\mu}{U_0} & \text{for } V_0 = 0 \\ \dfrac{\mu}{U} & \text{for } V_0 > 0 \\ \dfrac{\mu}{U} + \dfrac{1}{U}\dfrac{\partial U}{\partial x} & \text{for } V_0 < 0. \end{cases} \tag{15}$$

We have plotted these as functions of x in Figure 4b using $\mu = 10^{-7}$ s^{-1}, $U_0 = 5$ cm/s, $V_0 = \pm 20$ cm/s, and $Y = 200$ km. With this value for μ, two-thirds of the larvae disappear from the population because of the various biological causes within 4 mo from hatching. Most values of μ in the literature (e.g., Sissenwine et al. 1983) tend to be higher (see, however, Peterson

and Wroblewski 1984), but it is important to remember that these also include the advective losses. We have therefore chosen a smaller value of μ to reflect only biological processes; alternate values of μ will be considered shortly. The graph shows the extreme situation where the inflow or outflow is uniform over the whole downstream distance. The decay rate with distance travelled is always increased for offshore flow. For onshore flow, the decay rate can be reduced below the "no-ring" case but only very far downstream ($x > 500$ km) where the flow rate down the shelf is huge ($U = 30$ cm/s). Since onshore flows of 20 cm/s over a 500 km stretch of shelf are not likely to occur, we can conclude that the spatial decay rate will be enhanced in both the regions of onshore flow and the areas with offshore flow.

The net result, when a stream of larvae moving down the shelf and declining in density due to biological losses encounters a stationary eddy, can be calculated by combining the result for offshore flow in the region $0 < x < D$ with the one for onshore flow in $x > D$ where the ring is centered at the point $x = D$. In Figure 5 we compare the solution without the eddy

$$\frac{N}{N_0} = \exp\left(\frac{-\mu x}{U_0}\right) \tag{16}$$

to that with the eddy

$$\frac{N}{N_0} = \begin{cases} \exp(-\mu\tau) & \text{for } 0 < x < D \\ \dfrac{U(D)}{U(x)} \exp(-\mu\tau) & \text{for } D < x < W \end{cases}, \quad \tau = \int_0^x \frac{dx'}{U(x')} \tag{17}$$

where W is the length of the shelf domain, taken to be 500 km. Most of the decrease in population density occurs in the onshore flow regime; the final density is only half of that which would occur in the absence of the eddy. In assessing the causes of the population decrease, it is clear that the physics and the biology play comparable roles: the decrease in density when there is no eddy is a factor of two during the transit down the shelf (Fig. 5). The changes in density which occur predominantly in the region of onshore flow when the currents are present, give another factor of 2.5 decrease. Note that recruitment cannot be inferred directly from these density patterns; we will address the implications for recruitment in the section on Moving Eddies below.

We summarize the impact of stationary rings for various values of the onshore-offshore flow rates and the scale length along the shelf impacted in Figure 6. Here we plot contours of the ratio of the population density far downstream of the eddy (N_∞) to that

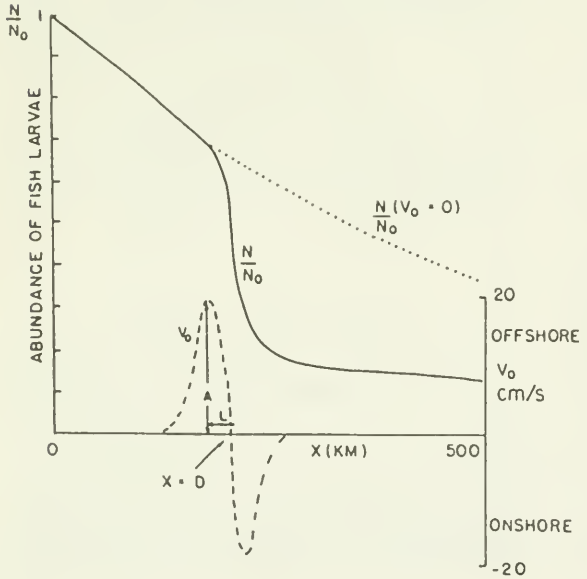

FIGURE 5. – Same as Figure 3 except biological losses ($\mu = 10^{-7}$ s^{-1}) are included.

which would be present without any cross-shelf currents (N_∞, $V_0 = 0$). This figure shows clearly the increasing impact with stronger transports onto or off of the shelf edge. There are slight differences in this ratio if the biological decay is ignored and if the cross-shelf flows occur over large distances, since the longshore flow slows down significantly. We should note that the decrease in larval fish density compared with the no-ring case depends on two nondimensional parameters $P_0 = AL/U_0Y$ and $P_1 = \mu L/U_0$. Thus for values of μ, U_0, or Y other than 10^{-7} s^{-1}, 5 cm/s, and 200 km, the graph can be read with suitable values of A and L to give the desired values for these two nondimensional numbers:

$$L_{\text{graph}} = P_1 \times 500 \text{ km} = \frac{\mu L}{U_0} \times 500 \text{ km}$$

$$A_{\text{graph}} = \frac{P_0}{P_1} \times 2 \text{ cm/s} = \frac{A}{\mu Y} \times 2 \text{ cm/s}.$$

MOVING EDDIES

In the previous examples, we have considered the changes in fish larvae distributions which occur when the shelf water flows by a stationary eddy. But rings frequently translate to the southwest, following a track between the continental slope and the Gulf Stream. The translational speeds vary considerably, ranging from a few cm/s to perhaps 10 cm/s. This along-shelf ring movement has a profound influence on the ring's contribution to decreasing the concentration of larvae – in some cases, they may be swept offshore in the entrainment flow of a slowly translating ring; in other cases the ring may catch up to, dilute, and pass the organisms. Finally, if the ring and shelf water are moving at the same rate, the larvae may never experience the impact of the ring, or alternatively may be in a region under constant influence.

The physical effects of a moving ring upon the larval fish population can be estimated readily from the previous results; it is only necessary to remember that the important quantity is the rate at which the shelf water moves relative to the eddy. If the ring is propagating westward more slowly than the westward drift of the shelf water, the organisms are in contact with the ring for longer periods of time, corresponding to a decreased value for the effective current U_0. But decreasing the effective downstream flow rate while keeping the eddy size constant is equivalent to increasing the length scale of the shelf region influenced by the ring's cross-shelf flows while the longshore current speed is maintained. Figure 6 shows clearly that such an increase in L will cause a greater reduction in larval density downstream of the eddy. As the eddy translation rate becomes closer and closer to the flow rate on the shelf (effectively increasing L in Figure 6), the effect upon the population becomes larger and larger, until eventually the eddy is drawing all of the larvae off the shelf as it passes. This occurs when the ring's speed is great enough so that the longshore transport of water relative to the ring is smaller than the offshore transport induced by the currents at the shelf edge:

$$U_0 - c < \int_0^x \frac{V_0(x')}{Y}\, dx' \qquad (18)$$

where c is the speed of translation of the ring.

If the ring is moving faster than the shelf currents, the situation is somewhat different; now the eddy catches up to the larvae and they are first influenced by a region of onshore flows and then by offshore currents. We can calculate the impact upon the population using the same methods as were employed in deriving Equation (10). For simplicity, we consider a domain which is infinite in x and compare the population density in regions which have not felt the ring with that in regions which have passed through the ring. For a ring moving at speed c, the equations describing the effects of the currents upon the population are

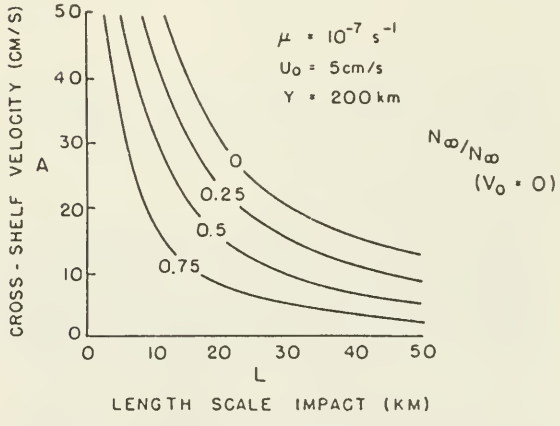

FIGURE 6. – The ratio of the number of larvae present far downstream of the eddy N_∞ to the number present if there were no eddy, $N_\infty(V_0 = 0)$. Contours of the ratio are plotted for different values of eddy size (L) and cross-shelf velocity A.

$$\frac{\partial}{\partial x}[(U-c)N] = \begin{cases} -V_0 \dfrac{N}{Y} & \text{for } V_0 > 0 \\ 0 & \text{for } V_0 < 0 \end{cases} \qquad (19)$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y}$$

and the population change caused by the eddy when the downstream flow is sufficiently faster than the ring's translation rate is

$$\frac{N(\infty) - N(-\infty)}{N(-\infty)} = \frac{1}{Y}\int_{V_0>0} \frac{V_0(x,0)}{U_0 - c}\,dx,$$

$$c < U_0 - \frac{1}{Y}\int_{V_0>0} V_0\,dx. \qquad (20)$$

When the flow stagnates relative to the ring at some point, we have

$$N(\infty) = 0 \qquad U_0 - \frac{1}{Y}\int_{V_0>0} V_0\,dx < c < U_0 \qquad (21)$$

and when the ring is moving faster than the shelf waters

$$\frac{N(-\infty) - N(\infty)}{N(\infty)} = \frac{\dfrac{1}{Y}\displaystyle\int_{V_0>0} V_0\,dx}{c - U_0 + \dfrac{1}{Y}\displaystyle\int_{V_0>0} V_0\,dx}$$

$$c > U_0. \qquad (22)$$

These are plotted in Figure 7. Notice that the ring may cause substantial losses in the population, especially when its speed is roughly matched to the mean flow on the shelf.

In principle, one could write down an analytical solution to the full problem (Equations (8) and (9)), including a translating ring and a time-dependent source at the upstream edge of the domain. However, this is a rather cumbersome calculation, and we have chosen instead to solve these equations numerically and simply present representative pictures here of the ring induced effects when a cohort – a single patch of larvae spawned roughly simultaneously – moves down the shelf and is disturbed by a ring. Some care is necessary in selecting a numerical scheme, since centered differencing is

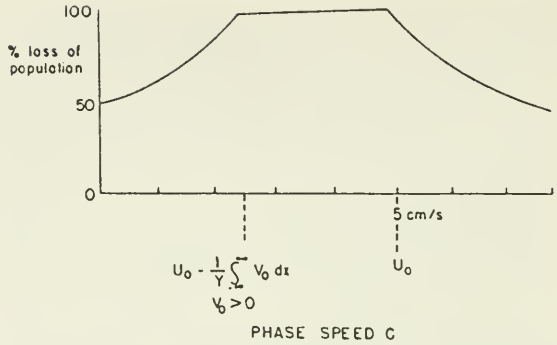

FIGURE 7.–Percent of the total number of larvae produced at the spawning site which are ultimately lost when a moving eddy is present at the shelf edge. When the speed c of the eddy is greater than $U_0 - 1/Y \int^X V_0$, all the larvae advected along the shelf are drawn offshore. When the ring is moving faster than the down-shelf current U_0, the ring catches up to the larvae, which are then diluted before being drawn offshore.

unstable while upstream differencing introduces a numerical diffusivity (Roache 1972). This may not be undesirable, since in reality one would expect some mixing to occur along the shelf; but unfortunately the diffusivity is spatially variable, being lowest in the vicinity of the eddy, and this we do not want in the model. We compromised by choosing a very small grid scale (5 km) so that the effective diffusivity is only 1.2×10^6 cm^2/s. This is not completely negligible, as shown in Figure 8a which plots successive snapshots of the larval fish density at 15-d intervals in the absence of any rings (the time step was one-half day). The population at the beginning of the domain is assumed to enter in a pulse

$$N_0(t) = \exp\left[-\frac{1}{2}\left(\frac{t}{5\text{ d}}\right)^2\right]. \qquad (23)$$

The gradual decrease in the peak abundance and the spread in width is caused by the numerical diffusion. Also included in this figure are the simple cases adding biological decay (Fig. 8b), a stationary ring (Fig. 8c), or both simultaneously (Fig. 8d). Note the large decreases in density induced as the population passes the ring and also the slower advection of the population down the shelf so that the organisms downstream are half a month older than they would otherwise have been (compare Figure 8b and 8d).

Finally, we show in Figure 9 two cases when a moving ring interacts with a patch of larvae. In the first case, the eddy is moving at 7 cm/s (faster than the 5 cm/s drift rate of the shelf water), so that the eddy catches up to the population and passes by it.

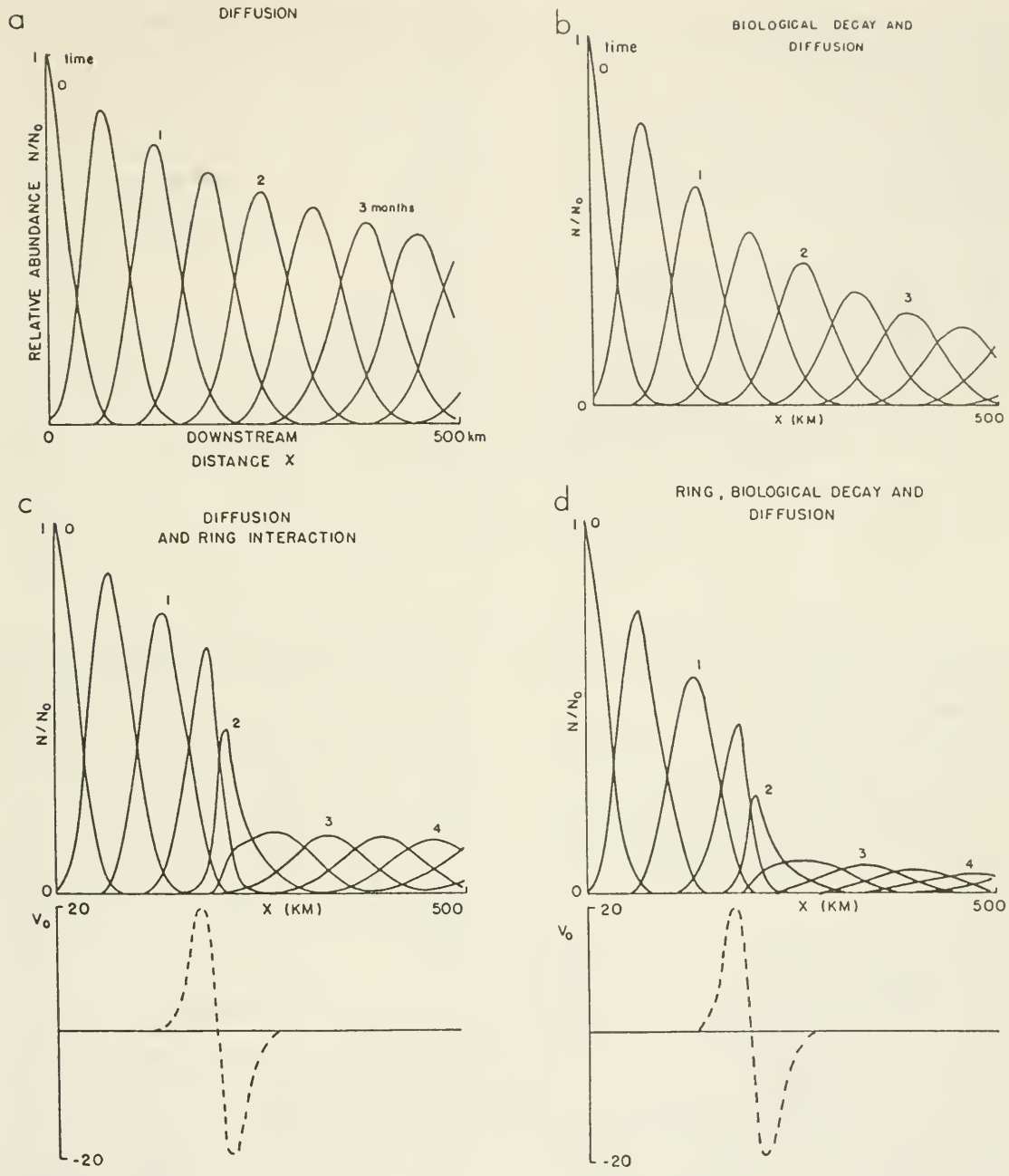

FIGURE 8.—Time-dependent solution of the numerical model which includes a) the diffusion of a spawning group or cohort of larvae as the patch is advected down the shelf. Snapshots are at 15-d intervals. Parameters $\mu = 0$, $U_0 = 5$ cm/s, $\Delta x = 5$ km, and $\Delta t = 0.5$ d. b) Same as (a) except $\mu = 10^{-7}$ s^{-1}. c) Same as (a) except a stationary ring is present at the shelf edge, with parameters A = 20 cm/s and L = 20 km. d) Same as (c) except $\mu = 10^{-7}$ s^{-1}.

As the ring passes by, the patch of larvae is spread out and distorted. Some losses do occur, but because of the rapidity of the interaction, these are slight. Comparison of this picture with Figure 8d shows that the larval density at 4 mo is higher than that for the stationary ring case. On the other hand, in the case when the shelf flow is faster than the speed of the ring (Fig. 9b), the impact of the ring is tremen-

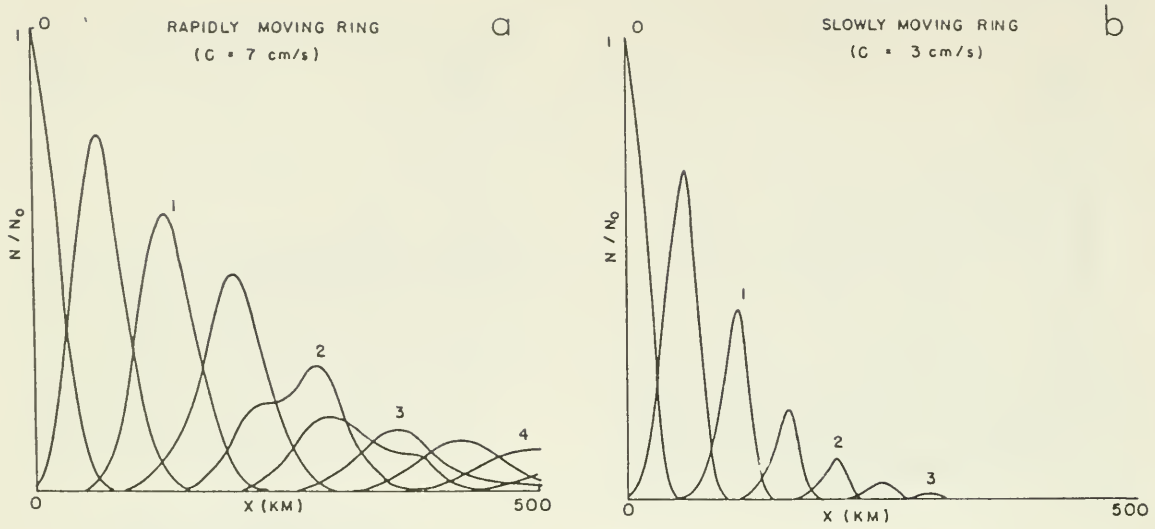

Figure 9.—a) Same as Figure 8d except a moving ring is present at the shelf edge, with parameters A = 20 cm/s, L = 20 km, and c = 7 cm/s. b) Same as (a) except c = 3 cm/s.

dous. When the population catches up to the back side of the eddy, the relative speed is so slight that all of the organisms are diverted off the shelf and lost from the system.

In addition to the plots of density versus time and along-shelf distance, it is extremely useful to consider the net balances for larvae within the domain. By integrating Equation (8) over x and t, using Equation (9) to evaluate the starting point contribution at $x = 0$, we can calculate the percentages of the total incoming population which are removed from the domain by three processes. First, there are biological decreases of the net population (due to the integrated μN term). It is important at this point to recall that we consider this as representing both larval death and metamorphosis. Therefore the recruitment should be roughly proportional to this term. (We do not consider the development time history of the larvae here; clearly this model could be combined with more detailed and complex larval development models to attempt more sophisticated recruitment predictions.) Secondly, there are losses due to advection off the shelf by the ring currents, and thirdly, larvae can be lost out the downstream end of the domain. The 500 km length of the domain puts the end of the model region near Cape May; exiting larvae may be swept offshore into the Gulf Stream and, like those drawn off by ring currents, presumably be lost.

The magnitude of each of these terms is summarized in Table 1 for the cases plotted in Figures 8b, d and 9a, b. Table 1 shows that the ring-induced advective losses from the population can be as large as or larger than the biological (mortality and metamorphosis) losses. This is most dramatic when the ring is moving slightly slower than the shelf water currents. The recruitment should vary in a fashion similar to the integrated biological causes term in Table 1; thus we expect a strong year class when rings are not interacting with the shelf waters, a reduction when stationary or rapidly moving rings are present, and a very sharp decrease in recruitment if a slowly moving ring is near the edge of the shelf at the time of spawning and larval development.

DISCUSSION

Theoretically, the passage of warm core rings close

TABLE 1.—Percent of total larval fish population entering the domain. WCR = warm core ring.

In the presence of	Biological causes	Advection off the shelf in flows induced by a WCR	Advection out of the downstream end of the domain
No ring $\mu = 10^{-7}\ s^{-1}$	62	—	38
Stationary ring A = 20 cm/s L = 20 km	42	46	12
Rapidly moving ring c = 7 cm/s	54	29	17
Slowly moving ring c = 3 cm/s	18	82	0

to the continental shelf should have considerable influence on the abundance and distribution of shelf-water larval fish and consequently on their recruitment to the fishery. Our simple mathematical model suggests a major effect of the ring-induced cross-shelf flows is to cause decreases in the larval density ahead of the ring where there is onshore flow. In addition, water being drawn off the shelf in an entrainment feature behind the eddy can carry larvae away, constituting a significant loss to the shelf population.

Research scientists of the National Marine Fisheries Service are currently investigating the frequency of entrainment events and their impact upon the fisheries (A. Friedlander[3]). Here we shall briefly examine the published literature on ring distributions and larval fish surveys. We have used the schematic charts of sea surface temperature produced by NOAA and ONR (Office of Naval Research). All of these records are necessarily incomplete due to cloudiness in the imagery and the difficulties in inferring water motions from the surface features. We therefore will make a somewhat subjective estimate of ring importance by considering the persistence of various eddies and their closeness to the shelf.

Figure 10 is a composite of the observed MARMAP distributions of cod *Gadus morhua*, larvae in the shelf region near Georges Bank during the late winter and spring of 1977 (Smith et al. 1979). We have placed on this figure the approximate locations of the warm core rings shown on the Experimental Ocean Frontal Analysis Chart produced by the U.S. Naval Oceanographic Office for this period. Figure 11 shows the corresponding MARMAP distributions for haddock, *Melanogrammus aeglefinus*, larvae.

Four warm core rings had trajectory paths near enough to Georges Bank during the spring spawning period in early 1977 to have had significant impact upon the larval fish distributions according to the predictions of our model. In front of each ring shown on Figures 10 and 11, the concentration of larvae over the shelf appears to be relatively low, much as our model suggests would occur in areas of ring-induced onshore flow. There even appear to be indications of entrainment of larvae off the shelf behind rings 77E (Figs. 10c, 11c) and 77A (Fig. 11d). Unfortunately the MARMAP station grid does not extend beyond the 200 m contour, so that this cannot be confirmed from the historical data. Extending the MARMAP grid further offshore would be of great benefit in assessing losses of larvae both by rings and by other offshore transports. It is also not possible to differentiate between patchiness from concentrated spawning upon Georges Bank or other biological causes and ring-induced variations. Again this makes the relationship between theory and data difficult to assess.

Warm core ring 77A (Figs. 10, 11) is an example of a nearly stationary eddy, remaining adjacent to Georges Bank from 30 March to 25 May 1977. But according to our theory, ring 77E is potentially even more dangerous, since it slowly sweeps down the entire Georges Bank edge between 18 May and 6 July, moving at 3-5 cm/s. Drifting groups of larvae could have caught up to the back side of ring 77E and been drawn off the shelf.

The survival of larvae in 1977 was low, and the year class was weak for both cod and haddock (Serchuk and Wood 1981; Clark et al. 1982). In other years also, there appears to be a relationship between the frequency of ring interaction with Georges Bank during the winter and spring spawning season and subsequent year-class strength for both cod and haddock stocks (Table 2). Cod spawn on Georges Bank from December into May and haddock spawn from February into June (Smith et al. 1979). Therefore we have examined the 6-mo period from January to June each year from 1975 to 1979 for ring activity using the charts of Bisagni (1976), Mizenko and Chamberlin (1979a, b), Celone and Chamberlin (1980), and Fitzgerald and Chamberlin

TABLE 2.—Apparent relationship between years of less frequent WCR (warm core ring) interaction with Georges Bank during the winter and spring spawning season and strong recruitment of cod and haddock stocks.

Year	Recruitment Strength		No. of WCR's interacting during spawning season (Jan.-June)	Comments
	Cod	Haddock		
1975	Very good	Very good	1	Eddy 6 present February-April
1976	Weak	Weak	3	WCR 75I, 76A, and 76C detrimental; 76D too far offshore
1977	Weak	Weak	4	WCR 76F, 76G. 77A, and 77E all detrimental
1978	Good	Very good	1	WCR 78A present in May; 78B too far offshore
1979	Weak	Average	3	WCR 78I, 79A, and 79B detrimental

[3]A. Friedlander, Northwest Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, R.R. 7A, Box 522A, Narragansett, RI 02882, pers. commun. January 1983.

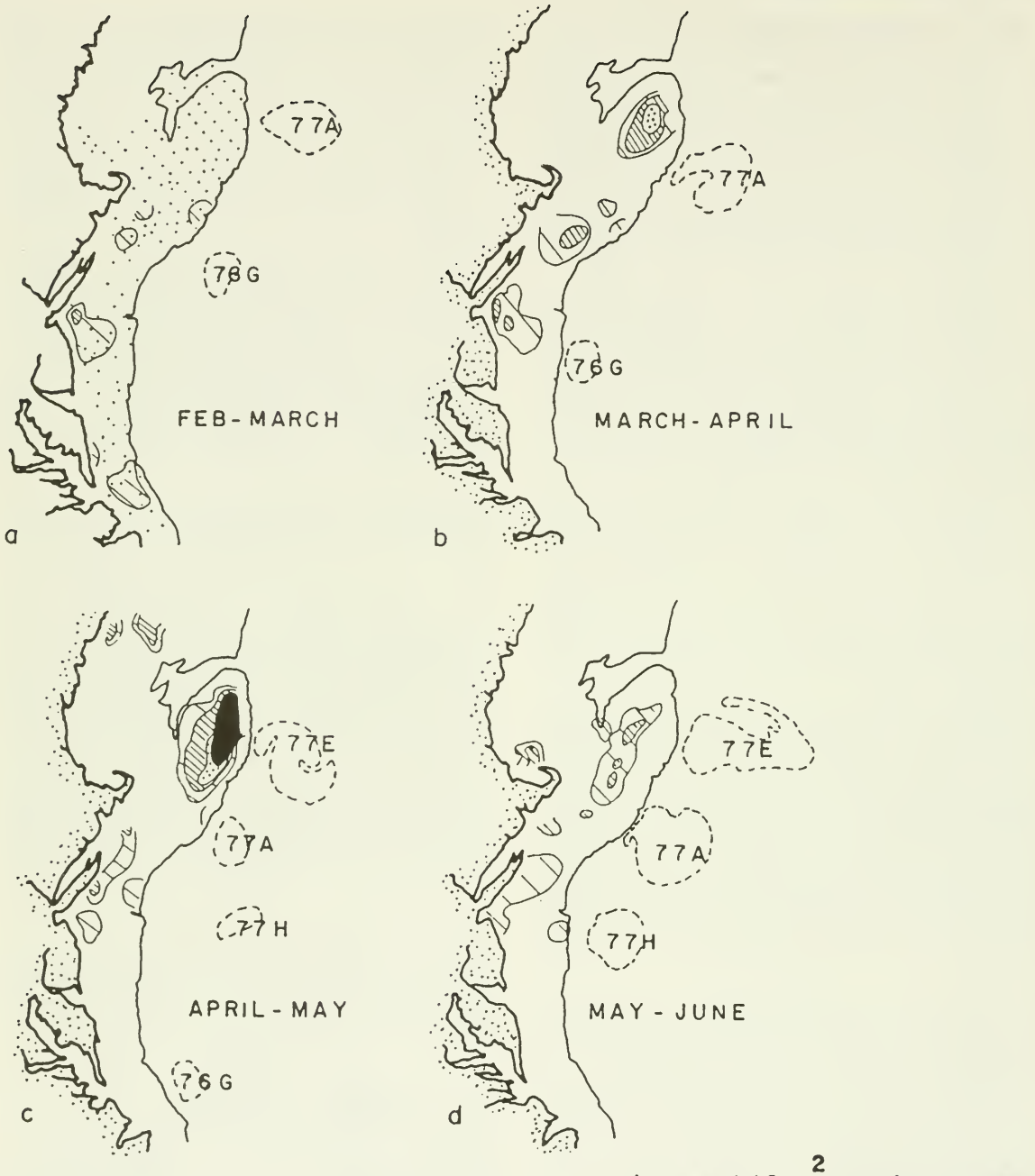

FIGURE 10.—Distribution and abundance of Atlantic cod, *Gadus morhua*, larvae off the eastern United States during the latter part of the 1976-77 spawning season (redrawn from Smith et al. 1979). The solid outline of the bottom topography is the 200 m contour. The positions of warm core rings 76G, 77A, 77E, and 77H are replotted from Experimental Ocean Frontal Analysis Charts produced by the U.S. Naval Oceanographic Office on 25 February (a), 23 March (b), 27 April (c), and 25 May (d) in 1977. The dots on (10a) show the sampling locations.

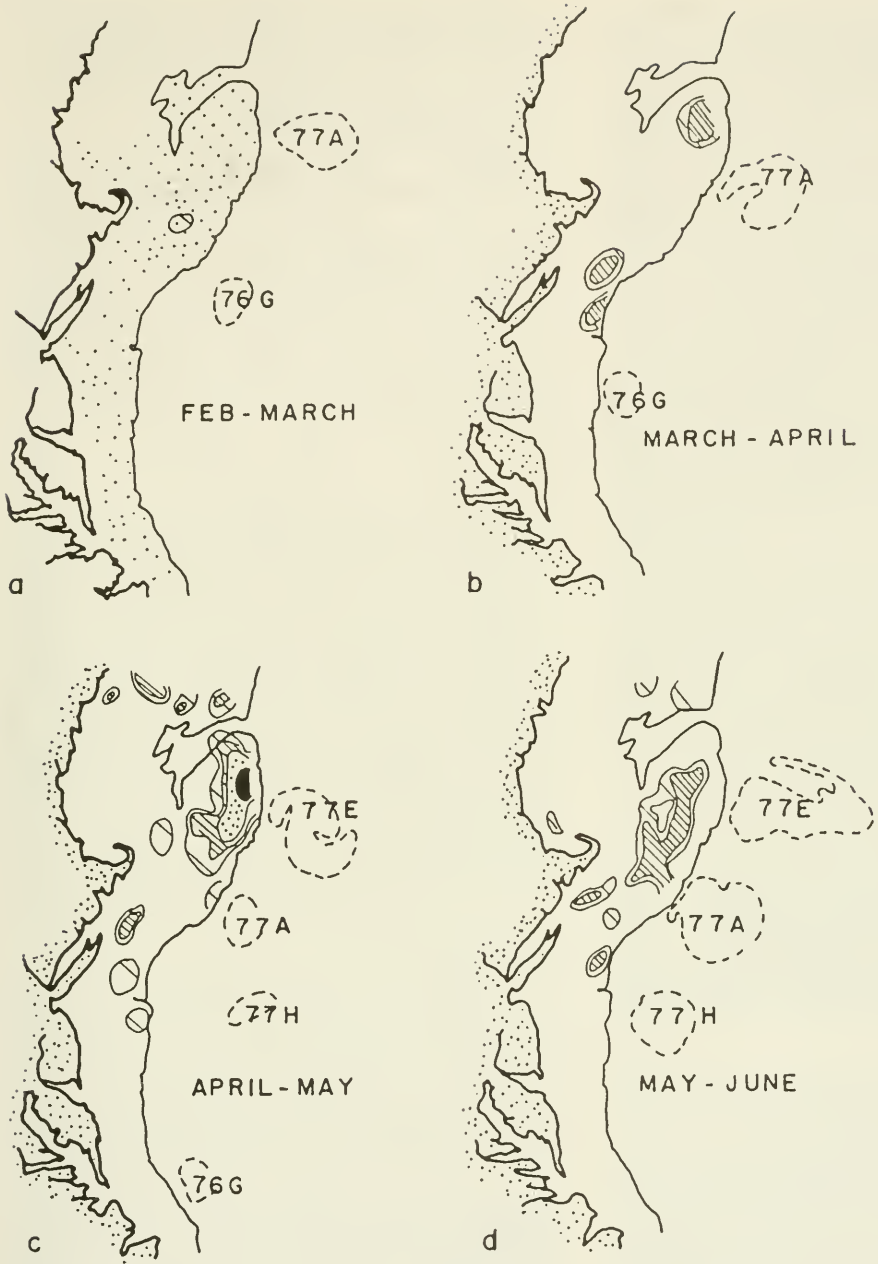

FIGURE 11.—Distribution and abundance of Atlantic haddock, *Melanogrammus aeglefinus*, larvae off the eastern United States during the latter part of the 1976-77 spawning season (redrawn from Smith et al. 1979). The positions of the warm core rings are the same as in Figure 10.

(1981). The number of rings present in the Slope Water is less important than the trajectories of the rings. If they pass too far offshore or appear too early or too late in the spawning season, they may have little impact. It is difficult to measure the magnitude of the onshore-offshore flows from the remote sensing data, but we have tried to consider the size of the shelf edge affected and the longshore speed of the eddy when judging the strength of a particular interaction. Unfortunately, we have no information for the years considered on the timing or location of spawning which undoubtably is important in determining the impact of individual rings.

The spring of 1975 was a time of low warm core ring activity (Table 2), and both cod and haddock produced good year classes, essentially the best since the 1960's (Smith et al. 1979). This high recruitment was not due to large numbers of larvae being spawned; indeed, the abundance of cod and haddock larvae was at a 5-yr low (Smith et al. 1979). Apparently, the few larvae present on Georges Bank experienced exceptionally high survival. There was only one ring (designated eddy 6 by Bisagni 1976) which by our model predictions could have influenced recruitment. Eddy 6 was in the vicinity of Georges Bank from February through April but did not seem to be entraining shelf water for this entire period.

During the spring of 1976 there were three, possibly four, warm core rings interacting with Georges Bank between January and May. Mizenko and Chamberlin (1979a) presented the track lines for eddies 75I (which later possibly became 76B), 76A, and 76C. Rings with these trajectories had the potential to affect recruitment. The 1976 year class strength for both cod and haddock stocks was weak (Smith et al. 1979).

The spring of 1977 was a year of unusually high ring activity. Figure 1 shows five rings (77A, 77C, 77E, 77G, and 77H) simultaneously present in the Slope Water region on 11 May 1977. Mizenko and Chamberlin (1979b) presented trajectories for all the eddies observed in 1977. Of these rings, 76F, 76G, 77A, and 77E appear to be most detrimental. The 1977 year-class strength for both cod and haddock stocks was again weak (Serchuk and Wood 1981; Clark et al. 1982).

The relationship of low ring activity and high recruitment observed in 1975 holds true again for 1978. This was a good year for cod and a very good year for haddock recruitment (Serchuk and Wood 1981; Clark et al. 1982). Examining the trajectories of warm core rings present during 1978 (Celone and Chamberlin 1980), we find no rings interacting with Georges Bank until late May or June. During the 60-d period from mid-February to mid-April, no anticyclonic eddies were apparent off the northeast coast. In late April and May, there were two rings (78A and 78B), but they occurred too far south or too far offshore to affect the Bank.

Finally in 1979, the most recent year for which there are both fisheries recruitment data and trajectory records, we find three potentially dangerous rings: 78I, impinging upon Georges Bank from March to July (Fitzgerald and Chamberlin 1981) and two eddies, 79A and 79B, lingering southwest of the Bank from February through May. The 1979 year class was weak for cod and only average for haddock (Serchuk and Wood 1981; Clark et al. 1982).

CRITIQUE

According to our calculations, warm core rings may have considerable influence on the distribution and ultimate survival of cod and haddock larvae spawned on Georges Bank. Our simple mathematical model demonstrates the possible effects of cross-shelf flows induced by a ring upon larval fish distributions and abundance. The ring's size, strength, and translation speed are critical in determining its potential impact. A stationary ring may cause a 20 to 50% loss of larvae by inducing advective transport off the shelf. If a ring is moving, the impact can be even greater, especially for an eddy travelling longshore at a slightly slower speed than the shelf water. In this most catastrophic case, a group of larvae can catch up to the back side of the eddy and be entirely swept off the shelf.

In briefly examining the published literature on ring trajectories and fisheries recruitment statistics, we have found what appears to be a relationship between years of frequent ring interaction with Georges Bank during the late winter and early spring spawning season and weak year classes of cod and haddock. Our analysis can be criticized as cursory and incomplete since we had no detailed information on entrainment features or on many important biological factors such as the timing and location of spawning. Future studies may show this relationship was fortuitous; however, our results certainly indicate that future study is warranted.

An implicit assumption in our analysis of ring events and fisheries recruitment data is that advective losses can affect year-class success. This has not yet been demonstrated for the Northwest Atlantic; however, Parrish et al. (1981) presented convincing arguments that the dominant exploitable fishes off the west coast have adopted spawning behaviors which minimize losses due to offshore transport.

They suggested that deviations from normal transport conditions may be a cause of the very large recruitment variations observed in the fisheries for sardine and anchovy. Whether warm core rings represent anomalous conditions or whether the shelf fishes of the Northwest Atlantic have adopted spawning patterns which minimize the losses by entrainment is yet to be discovered.

G. Laurence[4] has suggested that in some instances vertical migratory behavior may prevent significant numbers of larvae from being advected offshore. If the entrainment feature is shallow and the fish larvae avoid the surface layer, then the offshore transport could be much less than predicted by our model. The National Marine Fisheries Service is currently surveying entrainment features associated with warm core rings to assess the losses occurring off the shelf. Recently, Wroblewski and Cheney (1984) reported finding significant numbers of the white hake, *Urophycis tenuis*, larvae 140 km seaward of the Scotian Shelf break in Slope Water which had been entrained by a warm core ring. *Urophycis tenuis* spawn on the Scotian Shelf and upper continental slope. Wroblewski and Cheney concluded that the ring altered the usual larval drift pattern along the shelf edge. Curiously, no larvae of cod or haddock, which also spawn on the shelf during spring and summer, were found in the ichthyoplankton net tows. It remains to be demonstrated whether sufficient numbers of shelf-spawned larvae are transported offshore by rings to affect recruitment of shelf stocks.

The advective losses predicted by our model may be overestimates if only larvae present near the shelf edge are susceptible to entrainment and if their density is much lower than that further inshore. The influence of the ring may not reach the shallower regions where many larvae are found. Also, biological losses may be larger than assumed in the model, so that the relative importance of ring-induced losses may be less.

Warm core ring entrainments are not the sole mechanism by which fish larvae can be transported off the shelf. In 1955, Chase found a relationship between haddock recruitment and the strength of the wind-driven current normal to the southern side of Georges Bank. We also recognize that there could even be beneficial effects to the Georges Bank ecosystem if the ring-induced cross-shelf flows push nutrient-rich Slope Water onto the Bank and fertilize the system (G. A. Riley[5]). Rather than exploring all mechanisms, we have chosen to assess one particular source of variability which may contribute to fluctuations in year-class strength for the fish stocks spawning on Georges Bank.

We have also assumed that the fish larvae are well mixed across the shelf, although we know that they are generally distributed in patches. Thus our model solutions may be comparable with field data only if one integrates the field data over x and z as we have done in our simplified model. Fisheries recruitment data naturally reflects this integration over large spatial scales and we are encouraged by the apparent relationships in Table 2. However, loss during the larval period is only one factor affecting recruitment. Events during the postlarval stages are also significant; Sissenwine et al. (1983) showed that predation in these later stages is an important factor in year class success.

Our model has given quantitative but crude estimates of the importance of ring events for larval survival and suggested that the impact of the ring depends strongly upon its motion; investigations with more highly resolved and more complex models and further survey work for assessing both ring and mesoscale eddy influences on larval fish distributions and subsequent recruitment are the next steps.

ACKNOWLEDGMENTS

This research was supported by U.S. National Science Foundation grant number OCE-8019260 to G. R. Flierl and J. S. Wroblewski and by National Sciences and Engineering Research Council of Canada grant number A 0593 to J. S. Wroblewski.

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FIELD AND LABORATORY ASSESSMENT OF PATTERNS IN FECUNDITY OF A MULTIPLE SPAWNING FISH: THE ATLANTIC SILVERSIDE *MENIDIA MENIDIA*[1]

DAVID O. CONOVER[2]

ABSTRACT

Patterns in fecundity (i.e., spawning frequency, batch fecundity, annual egg production) of a multiple spawning fish, the Atlantic silverside, *Menidia menidia*, were assessed by 1) gonadal analysis of field specimens, 2) visual observations of spawning periodicity in the field, and 3) laboratory experiments. The gonadal analysis assumed that the difference between total number of eggs (recruitment + mature) per female just prior to the beginning of spawning, and recruitment egg retention per female at the end of the spawning season, represented annual egg production. Annual egg production estimated in this manner was 893 ± 197 eggs/g ovary-free body weight (±95% C.L.). Batch fecundity (no. eggs in the most advanced size class/g ovary-free body weight, ±95% C.L.) varied significantly during the breeding season, being lowest near the beginning (179 ± 21) and end (181 ± 28), and highest during the middle (266 ± 34 and 267 ± 23) of the breeding season. Batch fecundity averaged over the entire breeding season, was about 225 eggs/g ovary-free body weight, indicating that each female must spawn about four times. The gonadal estimate was tested by inferring the actual spawning frequency from daily, visual observations of spawning in the field. These observations showed that spawning occurred on a fortnightly cycle coincidental with new and full moons, and that each female spawned at most once per semilunar period. There were about four semilunar spawning phases during the breeding season, indicating close correspondence with the results of gonadal analysis.

Laboratory observations demonstrated that female *M. menidia* are physiologically capable of spawning more frequently than in nature. Total egg output in the laboratory was about twice that in the field.

Accurate estimates of fecundity are important in describing the dynamics of fish populations. In some fishes, all eggs mature synchronously and are shed in a single batch over a relatively brief period of time each year (Bagenal 1967). Estimating fecundity in such species is a simple process of enumerating the number of ripening eggs per female. However, in many other fishes, ova mature in multiple batches that are spawned successively within one spawning season. These species have been termed multiple spawners, batch spawners, serial spawners, or fractional spawners by various authors (Bagenal and Braum 1971; Hempel 1979; DeMartini and Fountain 1981; Gale 1983; Snyder 1983). Little is known about the patterns in fecundity of multiple spawners, even though many marine and freshwater fishes from diverse taxonomic groups in both temperate and tropical regions produce eggs in this manner. Determination of annual egg production in multiple spawners is difficult and recent studies have indicated that in some species, previous assessments may be in error by as much as an order of magnitude (Hunter and Goldberg 1980; Hunter and Leong 1981; DeMartini and Fountain 1981).

Frequency distributions of egg size (diameter) within ovaries of multiple spawning fishes are characteristically multimodal (Hempel 1979). In most multiple spawners, a synchronously maturing batch of eggs that is accumulating yolk sequentially arises from a much larger group of previtellogenic immature eggs, termed "recruitment" ova (Clark 1925; Bagenal and Braum 1971; Jones 1978; Hunter and Leong 1981). The problem in estimating fecundity has been to determine how many modes or batches of eggs are spawned annually. The conventional approach has been to count only the largest eggs or those above an arbitrary size (e.g., all yolked eggs) under the assumption that smaller eggs would be resorbed or spawned in later years. Whenever this assumption is incorrect, fecundity can be grossly underestimated. A second approach has been to infer the spawning frequency of adults from the proportion of field-collected females in ready-to-spawn condition (i.e., those containing hydrated eggs, e.g., Demartini and Fountain 1981) or from females showing evidence of having just spawned (i.e.,

[1]Contribution No. 89 of the Massachusetts Cooperative Fishery Research Unit, University of Massachusetts, Amherst, MA, and Contribution No. 437 of the Marine Sciences Research Center, State University of New York, Stony Brook, NY.

[2]Marine Sciences Research Center, State University of New York, Stony Brook, Long Island, NY 11794.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

presence of 1-d-old postovulatory follicles, observed histologically, Hunter and Goldberg 1980). Spawning frequency is then multiplied by batch fecundity (number of eggs in the largest size class) to arrive at annual fecundity. Excellent examples of this methodology can be found in DeMartini and Fountain (1981), Hunter and Goldberg (1980), and Hunter and Macewicz (1980). A third technique for estimating fecundity in multiple spawners has been laboratory experiments where females are confined and allowed to spawn repeatedly (Gale and Gale 1977; Gale and Buynack 1978, 1982; Hislop et al. 1978; Gale 1983). The problem here is that spawning frequency and fecundity are dependent on the food supply (Wootton 1973, 1977, 1979; Townshend and Wootton 1984), so that it may be difficult to interpret laboratory data unless detailed studies of feeding rate and/or fecundity of fish in nature have been previously conducted (e.g., Hunter and Leong 1981).

The ovarian cycle of many fishes that breed during a restricted season involves two major, alternating phases of oocyte production and growth: 1) a previtellogenic phase during which new oocytes are produced, cell organelles form, and cytoplasmic growth occurs; and 2) a vitellogenic phase during which growth is faster and yolk accumulates in the ovum (Ball 1960; Jones 1978; Tokarz 1978; Baggerman 1980). The greatest production of new oocytes and phase one growth occurs during the postspawning season, with vitellogenic growth and maturation of eggs occurring just prior to and during the spawning season (this may not be true in tropical or other fishes that breed throughout most of the year, see reviews by Ball 1960; Jones 1978; Baggerman 1980). Hence, in multiple spawners having a restricted breeding season, the reservoir of recruitment eggs may be largely formed prior to the breeding season. If true, then the number of recruitment eggs per female should consistently decline as the breeding season progresses. The rate of decline in number of eggs per female would provide an estimate of seasonal egg production, and spawning frequency per female could be estimated from the total number of eggs shed divided by batch fecundity. The method could be tested by comparing the estimated spawning frequency with the actual spawning frequency determined independently in some other manner.

The purpose of this paper is to describe patterns of batch fecundity and annual egg production in the Atlantic silverside, *Menidia menidia*. The analysis employs the method described above: I show how the total number of eggs per female (recruitment + maturing) present at the beginning of the spawning season minus recruitment eggs per female retained at the end of breeding can be used as an estimate of total egg production. The method is tested by showing that predicted spawning frequency is identical to the spawning frequency inferred from direct visual observations of spawning periodicity in a field population. Observations of spawning frequency and egg production under laboratory conditions are used to demonstrate that individual females are physiologically capable of maintaining the egg production rates and spawning frequency estimated from field populations.

The Atlantic silverside, *Menidia menidia*, (Pisces: Atherinidae) is a multiple spawning marine fish that inhabits coastal waters of eastern North America (Middaugh 1981; Conover and Kynard 1984). *Menidia menidia* is an annual fish: all individuals mature at age 1 and < 1% of breeding populations are 2 yr old. The ecological importance of *M. menidia* in terms of biomass transport from salt marsh to offshore communities and as forage for piscivorous fishes has been previously documented (Bayliff 1950; Conover and Ross 1982; Conover and Murawski 1982). The Atlantic silverside is an excellent species for studying patterns in fecundity because it is numerous and can be easily collected, spawning is easy to visually observe in the field, and it readily breeds in the laboratory.

METHODS

Gonadal Analysis

Field Sampling

Fish were sampled from the salt marsh region of Essex Bay, MA, with beach seines. Specimens were collected every 2 wk during 1977 as part of a general study of the population ecology of *M. menidia*. Additional specimens were collected intermittently in the spring during the breeding season. All collections were made in daylight within 1-2 h of low tide, and all specimens were immediately preserved in 10% buffered Formalin[3]. Detailed descriptions of Essex Bay and sampling methodology are available in Conover and Ross (1982).

Fecundity

Gonads were excised and weighed (nearest 0.01 g) from fish captured on 11 dates from October 1976 to July 1977. All fish were measured for total length

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(nearest millimeter) and gonad-free body weight (nearest 0.1 g). The gonadosomatic index (GSI) was calculated by expressing gonad weight as a percentage of total weight (Snyder 1983).

Preliminary microscopic examination of ripe ovaries from collections during the breeding season revealed three general egg types that corresponded with modes found in frequency distributions of egg diameters from ripe females (see Figure 1 below). The three egg classifications were defined by both size and appearance of the ova as follows:

Immature ova: spherical, 0.05-0.60 mm in diameter. The smaller ova in this group (0.05-0.15 mm) were primary oocytes with a clear cytoplasm and large nucleus. The larger ova (0.15-0.60 mm) were opaque and white. These ova formed one continuous mode in the frequency distribution so they were considered as one group (Fig. 1A, B).

Maturing ova: spherical, 0.6-1.0 mm in diameter, yellowish, and translucent.

Ripe ova: spherical, hydrated, 1.0-1.2 mm in diameter, hyaline and golden, with visible gelatinous threads coiled around the egg.

To confirm that these classifications represented distinct groups of synchronously maturing ova, I measured the diameter (random axis) of about 150 eggs, randomly subsampled from each of several females. In females captured during the breeding season, there were two distinct modes: the most advanced mode represented maturing eggs, and the other mode represented immature eggs (Fig. 1A). In females with ripe eggs, three modes in egg frequency were apparent: the most advanced group represented ripe eggs, the intermediate mode represented the next batch of maturing eggs, and the remaining mode consisted of immature eggs (Fig. 1B).

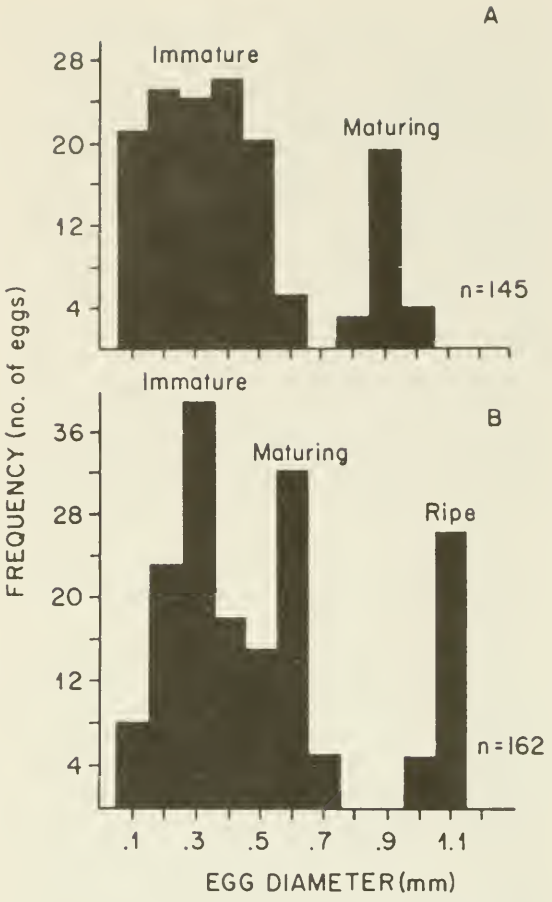

FIGURE 1.—Frequency vs. egg size (diameter in 0.1 mm intervals) for ova randomly sampled from two female *Menidia menidia* collected 6 June in Essex Bay, MA. A) A nonripe female in which there is a large number of immature eggs and a clearly definable mode of maturing eggs. B) A ripe female in which there is a large mode representing immature eggs, an intermediate mode of eggs beginning to mature, and an advanced mode of ripe eggs.

"Batch fecundity" was defined as the number of mature eggs in the most advanced size class, and presumably represented the number of eggs spawned at one time. As illustrated in Figure 1, the most advanced size class of maturing or ripe eggs was clearly distinguishable from, and did not overlap in size with, the immature ova. In ripe females, batch fecundity represented the number of hydrated eggs (e.g., the most advanced mode in Figure 1B). In nonripe females, batch fecundity represented the number of maturing eggs (e.g., the most advanced mode in Figure 1A). "Recruitment fecundity" was defined as the number of eggs smaller than the most advanced egg batch. Recruitment fecundity presumably represented the number of ova from which additional batches of mature eggs could potentially arise. In ripe fish containing three modes (e.g., Fig. 1B), the intermediate mode of eggs in early maturation was included with the immature eggs as part of the recruitment egg group because these overlapped in size with, and were difficult to separate from, immature ova. The minimum size of recruitment eggs was 0.05 mm in diameter. "Total fecundity" was defined as the sum of recruitment and batch fecundity.

Batch, recruitment, and total fecundity of individual females were estimated gravimetrically in the following manner. A cross section comprising 10-20% of the total ovarian weight was cut from a randomly chosen portion of one ovary. Both the sub-

sample and the remaining ovarian material were blotted on absorbent paper and weighed to the nearest milligram. The subsample was then placed in modified Gilson's fluid (Bagenal and Braum 1971), teased apart and vigorously shaken to separate ova, and stored for several weeks. All eggs in a subsample were counted and classified as belonging to either the recruitment pool or the mature batch of eggs. Batch and recruitment fecundities were then estimated for each female by multiplying the number of eggs in the subsample by an expansion factor (total ovarian weight/subsample weight). The mean diameter of the largest size class of eggs was also determined by measuring a random sample of about 20 mature eggs from each female. Shrinkage of eggs during preservation appeared to be minimal, so no correction for shrinkage was made. Fecundity was estimated for females collected on four occasions, from just before the beginning of the spawning season to its end. These dates were 6 May, 6 June, 22 June, and a pooled sample captured over the period 6-13 July.

To demonstrate whether estimates of fecundity were dependent on the location of the ovarian subsample, I compared these among replicate subsamples taken from the anterior and posterior sections of the right and left ovaries of six different females (i.e., four subsamples per female). Two-way ANOVA indicated that estimated fecundity was independent of subsample location ($P > 0.10$) and the coefficient of variation was low (CV = 4.2%). The ratio of the number of batch eggs to recruitment eggs was also independent of subsample location ($P > 0.5$). Moreover, I also directly counted the total number of batch eggs in four of the females used in the above analysis; in each case estimated batch fecundity was within 10% of the true value.

Field Observations of Spawning Frequency

The frequency of spawning in a natural population of *Menidia menidia* was inferred from daily, direct field observations of mating. The Atlantic silverside spawns in large groups of fish that broadcast milt and eggs amongst vegetation in the upper intertidal zone of salt marshes within 1 or 2 h of the daylight high tide (Middaugh 1981; Middaugh et al. 1981; Conover and Kynard 1984). At such times, spawning can be easily observed. My observations were conducted at a major spawning site in Salem Harbor, MA. Daily assessments of spawning intensity were conducted throughout the spawning season by counting the number of aggregations of spawning fish sighted during high tide. Methodological details are provided in Conover and Kynard (1984).

Laboratory Observations of Spawning Frequency and Egg Production

Spawning frequency and egg production were also assessed by confining fish in laboratory tanks. A summary of the experimental procedure, described fully in Conover and Kynard (1984), follows. A large group of *M. menidia* were captured at Salem Harbor on 5 May 1979 and transported to the University of Massachusetts marine laboratory at Gloucester, MA. One female and two male fish were placed into each of the four 74 L tanks at room temperature on a natural photoperiod. Four males and four females were also placed into each of two circular plastic pools (diameter 1.5 m, depth 0.3 m). These pools were located outdoors. All fish were fed fresh, chopped seaworms (*Nereis*) and amphipods in excess of daily consumption. Spawning substrates consisted of a small tuft of synthetic aquarium filter floss, anchored to the bottom of each tank or pool. The floss was checked several times daily for the presence of eggs. When eggs were discovered, the floss was replaced. All eggs were preserved and enumerated later. Eggs from each female were usually deposited in a distinct clump on the floss, providing a means for determining the number of females that had spawned in the previous interval. The experiment was allowed to continue until spawning ceased (27 July). Length and weight of spawners was measured at the conclusion of testing.

RESULTS AND DISCUSSION

Gonadal Analyses

In late fall, just prior to the offshore winter migration (Conover and Murawski 1982), ovaries represented about 1% of total body weight (Fig. 2) and contained only small (< 0.1 mm), clear, transparent eggs. Upon return of fish to the shore zone the following April, the ovarian GSI was about 4% and many opaque, white, immature ova (< 0.5 mm) were present. Of the 25 females captured on 6 May, 92% contained numerous immature ova and a clearly definable batch of maturing ova. The first female carrying ripe egges was collected on 12 May. The GSI peaked in both sexes on 25 May and declined thereafter until the end of July. The first fish in spent condition (no maturing egg class, recruitment eggs, if present, degenerating, GSI < 5%) was captured on 22 June. The proportion of spent fish was 23% on

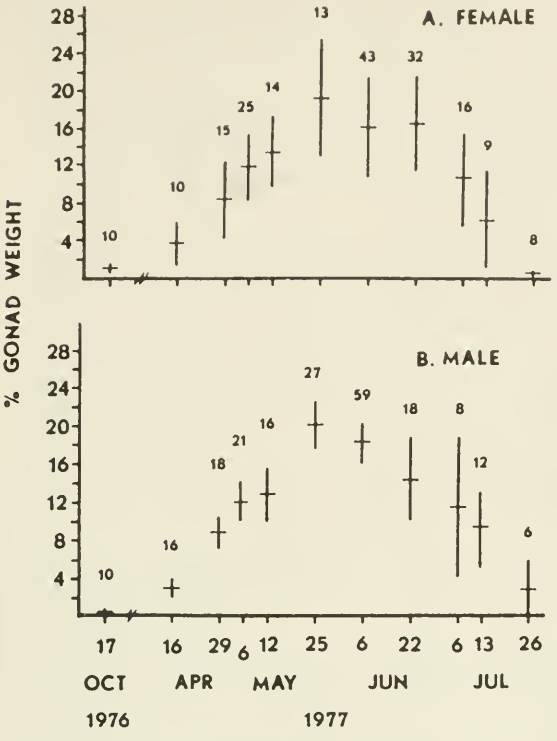

FIGURE 2.—Gonadosomatic index (gonad weight expressed as a percentage of total weight) for *Menidia menidia* collected during 1976-77 in Essex Bay, MA. The horizontal lines represent means, the vertical lines represent one standard deviation, and the sample size is given above the datum for each collection.

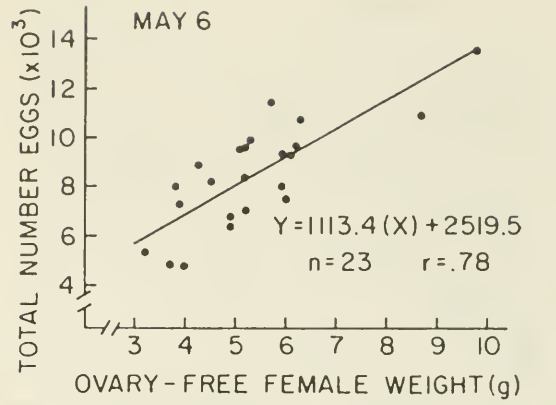

FIGURE 3.—Relation between total number of eggs (recruitment plus mature) and ovary-free female body weight for Atlantic silversides captured just prior to the beginning of the spawning season (6 May 1977) in Essex Bay, MA.

6-13 July and 100% on 26 July. Hence, the breeding season in Essex Bay began sometime after 6 May and was over by 26 July during 1977.

The potential annual fecundity of *M. menidia* may be represented by the total number of eggs (recruitment + maturing ova) within females just prior to the breeding season (i.e., 6 May), if additional immature eggs are not continually added to the recruitment pool as the spawning season progresses. If this premise is true, then there should be a continuous decline in recruitment fecundity and total fecundity during the breeding season (although not necessarily in batch fecundity).

Comparison of fecundities between sample dates was facilitated by the following observations. Total number of eggs per female was linearly related to ovary-free body weight (Fig. 3). Batch fecundity was also a simple linear function of ovary-free body weight (Fig. 4) and the rates of increase in batch fecundity, recruitment fecundity, and total fecundity with increase in female weight were generally similar among sample dates (i.e., regression slopes differed little, t-test, $P > 0.05$). Correspondingly, relative batch fecundity, relative recruitment fecundity, and relative total fecundity (relative fecundity = no. eggs/g ovary-free body weight) were each independent of body weight in nearly all tests (linear correlation, $P > 0.05$), suggesting that females of all sizes allocated about the same proportion of energy to reproduction. Hence, fecundity was adequately described and compared between dates if expressed as a proportion of ovary-free body weight, rather than as a function of weight.

Batch fecundity, recruitment fecundity, and total fecundity (no. eggs/g ovary-free body weight) during the spawning season are presented in Figure 5. Three patterns are evident. First, total fecundity and recruitment fecundity monotonically declined (Fig. 5A, B). Total fecundity was 1,609 ± 126 (95% C.L.) on 6 May and declined to 876 ± 177 by the second week of July (Fig. 5A) while recruitment fecundity was initially 1,430 ± 128 on 6 May and declined to 716 ± 164 in July (Fig. 5B). Second, batch fecundity differed significantly between sample dates, being maximal during the middle of the breeding season (266 ± 34 and 267 ± 23 on 6 and 22 June, respectively) and minimal at the beginning and end of the breeding season (179 ± 21 and 181 ± 28 on 6 May and 6-13 July, respectively; Fig. 5C). Third, many recruitment eggs remained in ovaries near the end of the spawning season (Fig. 5B) and most of these were probably resorbed soon thereafter because all females captured on 26 July contained only small (< 0.10 mm), transparent oocytes. Two females from the 6-13 July collection contained only immature eggs that appeared to be in a state of resorption and had no maturing egg group.

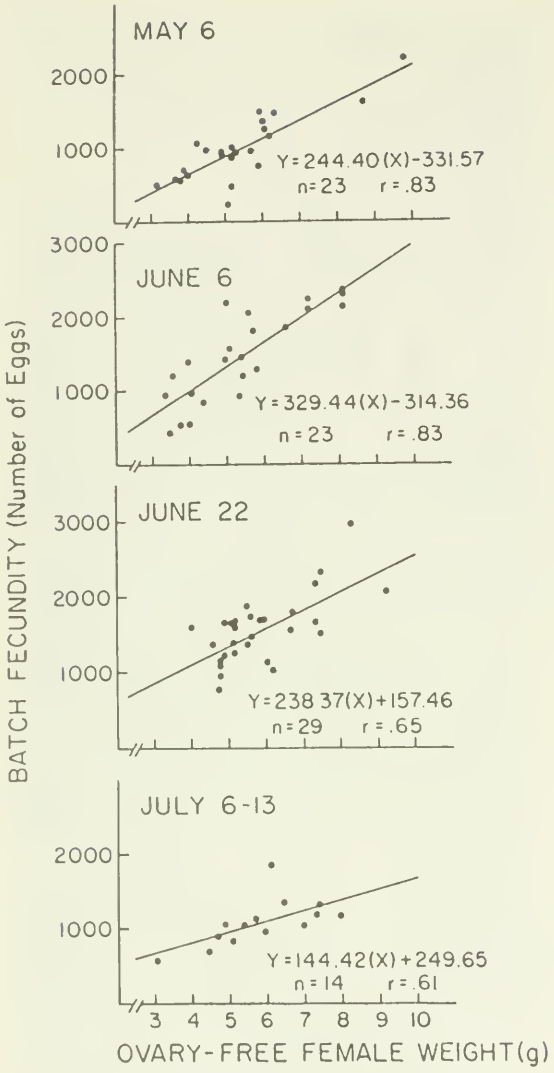

FIGURE 4.—Relation between batch fecundity (no. of eggs in the most advanced size class) and ovary-free female body weight for Atlantic silversides captured on four occasions during the 1977 breeding season in Essex Bay, MA.

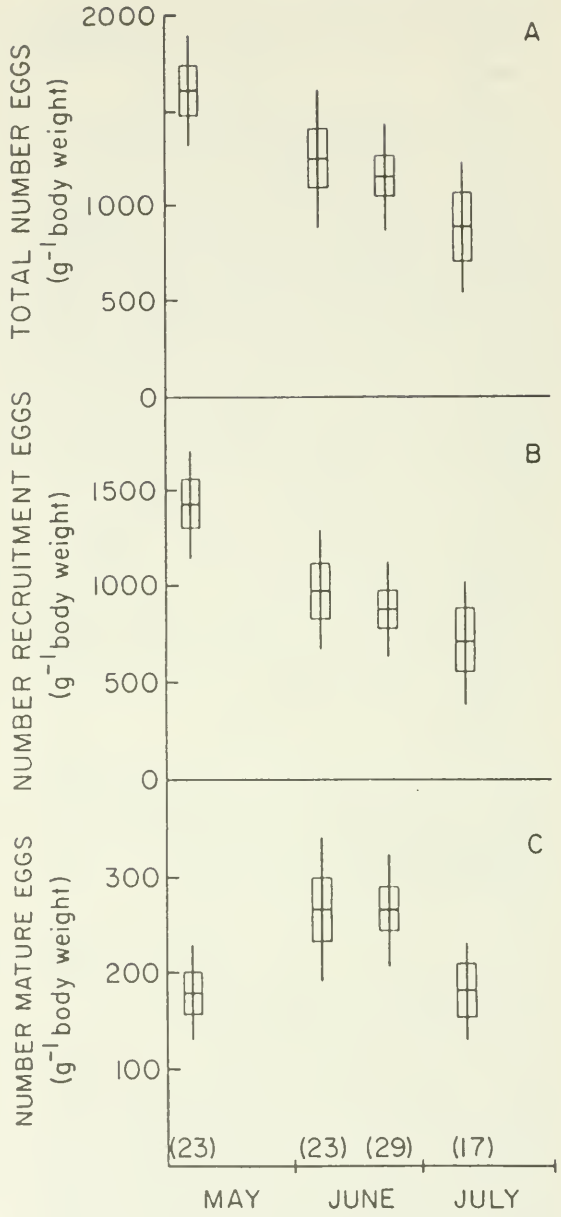

FIGURE 5.—Relative fecundity (no. eggs/g ovary-free female body weight) for Atlantic silversides captured on four occasions during the 1977 breeding season in Essex Bay, MA. The horizontal lines represent means, the vertical lines represent one standard deviation, and the rectangles represent 95% C.L. Sample sizes are in parentheses. All fish were spent on 26 July. A) Total number of eggs. B) Number of recruitment eggs (recruitment fecundity). C) Number of mature eggs (batch fecundity).

Batch fecundity as estimated above assumes that the number of eggs in the most advanced mode is not reduced by atresia as they grow and are eventually shed. I noted few eggs which appeared to be atretic or in a process of resorption (except near the very end of the breeding season) and females which had recently spawned usually contained few, if any, residual ripe eggs. Similar observations were reported by Clark (1925) for the atherinid *Leuresthes tenuis*. Moreover, if some eggs cease growing and are resorbed before reaching maturity, there should be a negative correlation between batch size and the mean diameter of eggs in the batch (i.e., no. batch eggs/g ovary-free body weight should generally be

lower in fish nearly ready to spawn than in fish where batch eggs are still maturing). Linear correlations of batch size and mean diameter of the maturing egg batch for each of the four dates on which fecundity was measured were nonsignificant ($P > 0.05$), suggesting that the number of eggs in a batch does not decline much as the oocytes grow to maturity.

Assuming that the recruitment pool of immature eggs is fully formed prior to the breeding season, an estimate of the actual number of eggs produced annually can be derived from the above data. Because recruitment eggs remain at the season's end, actual egg production is best represented by the total number of eggs present just prior to the beginning of the spawning season minus the number of recruitment eggs retained when the spawning season ends. For the above data, this provides a value of (1,609 ± 126) − (716 ± 164) = 893 ± 197 eggs/g ovary-free body weight (±95% C.L.). The mean body weight of females during the breeding season was 5.6 g so that the average female would have spawned about 5,001 eggs in a season. The mean batch fecundity over the spawning season was 223 eggs/g ovary-free body weight or about 1,249 eggs/female. Hence, if the initial assumption is correct, the average female must spawn about four times during the breeding season.

Frequency of Spawning in Nature

To test the prediction of spawning frequency derived above, spawning periodicity was determined from direct, visual observation of breeding events in the field. In 1978, I discovered a large spawning site in Salem Harbor, MA, where numerous eggs of *M. menidia* were deposited amongst mats of filamentous algae in the upper intertidal zone. Salem Harbor is located 20 km southwest of Essex Bay; however, individuals in each area are likely members of the same population because extensive mixing occurs during the offshore winter migration (Conover and Murawski 1982). Electrophoretic studies of geographic variation in *M. menidia* also support this contention (Johnson 1975).

Daily observations of the number of spawning aggregations sighted during high tide at Salem Harbor in 1979 showed that populations of Atlantic silversides breed on a semilunar periodicity coinciding with new and full moons (see figure 2 in Conover and Kynard 1984). Middaugh (1981) has reported similar observations based on a 3-yr study of populations in South Carolina. Within each semilunar spawning period of 1979 in Salem Harbor, the majority of spawning (40-90%) occurred on a single day, suggesting that females spawn, at most, once per semilunar cycle. This conclusion is further supported by the observation that sex ratios in spawning aggregations were highly male biased, whereas during nonspawning intervals, the sex ratio was near unity (Conover 1984). The sex ratio data is explained if females spawn, at most, once per cycle, while males spawn each day of a spawning period.

During 1979 in Salem Harbor, there were five semilunar spawning periods, although the first in late April was very light. In Essex Bay during 1977, there were four semilunar phases during the period defined as the breeding season. Hence, estimated spawning frequency based on gonadal analysis and direct observations of spawning fish agreed closely.

Spawning Frequency and Egg Production in the Laboratory

Females held in laboratory tanks, whether housed individually indoors or outdoors in groups where natural day and night illumination was present, did not maintain a fortnightly spawning periodicity. Instead, spawning occurred much more frequently: the interval between spawnings averaged about 4 d/female (Table 1; see also figure 4 in Conover and Kynard 1984). Batch fecundity averaged 99-187 eggs/g ovary-free body weight among different tanks. Total egg production averaged 1,425-3,375 eggs/g ovary-free body weight. Hence, the experi-

TABLE 1.—Egg production by *Menidia menidia* on unlimited food rations in the laboratory. Field data are also provided for comparison.

	No. of females	Mean ♀ body weight (g)	Days from 1st to last spawning	No. of egg batches per ♀	Days between spawn per ♀	No. eggs/g ♀ body weight per egg batch	Total eggs per ♀ (no.)	Total eggs/g ♀ body weight (no.)
Pool 1	4	6.32	63	15.25	3.9	99.0	9,551	1,511
Pool 2	4	5.82	51	11.75	3.7	121.2	8,299	1,426
♀ A	1	3.9	72	20.0	3.6	169.5	13,218	3,389
♀ C	1	3.6	[1]28	[1]7.0	4.0	187.0	[1]4,710	[1]1,308
Field	—	—	60-75	4.0	14-15	180-266	5,000	893 ± 197

[1]Low values reflect the fact that ♀ C died before the conclusion of the experiment.

mental fish responded to laboratory conditions by reducing batch fecundity somewhat, but spawning more frequently, and thereby producing about twice the number of eggs as in nature (Table 1). The daily rate of egg production was 24-47 eggs/g female body weight per d in the laboratory, but averaged about 14 eggs/g female body weight per d in the field.

At the termination of the experiment, four of the eight females in the outdoor pools were spent, three contained only recruitment eggs, and one had both recruitment and maturing eggs. Female A died of unknown causes after its last spawning on 22 July. Female C also died (9 June) before cessation of spawning by jumping out of the tank.

The total weight specific egg production for the experimental fish was generally within the range of total eggs available prior to the beginning of the breeding season. The one exception was female A which produced about twice the total number of eggs that a fish of its size should have had available at the beginning of the spawning season (see Figure 3). Hence, under certain laboratory conditions, females may be capable of producing new oocytes from oogonia during the breeding season, as recruitment eggs become depleted. These laboratory observations show that the reproductive patterns of egg maturation and spawning which are highly synchronized with and influenced by environmental factors in the field, easily become disrupted when individuals are removed from their natural habitat.

CONCLUSIONS

This study indicates that annual fecundity in *Menidia menidia*, and perhaps certain other fishes, can be estimated from the difference between total number of eggs (recruitment plus maturing) prior to the breeding season and recruitment egg retention near the end of the breeding season. Dividing the estimated total number of eggs shed per female by mean batch fecundity provided an estimate of spawning frequency. The accuracy of this value for spawning frequency was tested and found to agree closely with the spawning frequency inferred from direct field observations of breeding fish. Previous estimates of the fecundity of *M. menidia* were about 3-10 times less than that reported here because spawning frequency was not determined (Bayliff 1950; Jessop 1983). The studies of Hunter and his coworkers on northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Hunter and Leong 1981), and DeMartini and Fountain (1981) on queenfish, *Seriphus politus*, have amply demonstrated that estimates of annual fecundity can be in error by over an order of magnitude when multiple spawning is ignored.

The estimation of fecundity from the difference between total prespawning fecundity and recruitment egg retention is dependent on the assumption that new oocytes are not simultaneously produced from oogonia and added to the reservoir of recruitment eggs as mature eggs are spawned. Agreement between predicted and observed spawning frequency suggests that this may be true in *M. menidia*. Many more recruitment eggs were present in ovaries at the beginning of the spawning season than were actually spawned in nature. Evidently, the recruitment egg pool is largely formed before the breeding season in *Menidia*, as is believed for some other seasonal spawners (Tokarz 1978; Jones 1978; Baggerman 1980). However, the generality of this pattern in other multiple spawning temperate or tropical fishes is not clear. Clark (1925) noted that the relative abundance of mature, intermediate, and immature eggs in *Leuresthes tenuis* was relatively constant during the breeding season and concluded from this that new oocytes must be continuously produced to replenish those spawned. Taylor and DiMichele (1980) reached a similar conclusion based on the relative abundance of different developmental stages of oocytes during the semilunar spawning cycle of *Fundulus heteroclitus*. However, analyses based on relative proportions do not take into account that gonad weight (GSI) generally declines as the season progresses (e.g., Fig. 2) and that number of eggs in the most advanced mode is not necessarily constant during the breeding season. Comparison of the relative abundance of egg sizes from sections of an ovary may not reflect changes in absolute number. For example, the relative abundance of recruitment eggs in *M. menidia* during 1977 was 0.88 on 6 May, 0.78 on 6 June, 0.76 on 22 June, and 0.79 during 6-13 July. Hence, the relative proportion of recruitment eggs did not consistently decline during the breeding season even though the absolute number of eggs declined by a factor of 2.4. In any event, too little is known about patterns of oocyte growth in fishes to recommend that the annual fecundity of multiple spawners can generally be determined by monitoring the decline in the standing stock of ova as was done here. For instance, in tropical species that breed most of the year recruitment eggs may be produced continuously. Whenever possible, the results of several different approaches to estimating fecundity should be compared.

The results of the laboratory study demonstrated that *M. menidia* is physiologically capable of spawning much more frequently and over a shorter interval

than normally occurs in the field. The reasons for the higher spawning frequency and cumulative egg production for fish in captivity are probably several. Fecundity may have been increased because ration size was unlimited. Fecundity is dependent on the food supply in many species (Wootton 1979). In the stickleback, *Gasterosteus aculeatus*, (Wootton 1977) and the convict cichlid, *Cichlasoma nigrofasciatum*, (Townsend and Wootton 1984) experimental studies have demonstrated that the number of spawnings was positively related to food ration and the interval between spawnings was inversely related to ration.

In my experiments on *M. menidia*, spawning frequency may also have been increased beyond that in nature due to the continuous availability of appropriate spawning substrates and lack of tidal spawning cues in the laboratory. Conover and Kynard (1984) noted that both marine and freshwater populations of *Menidia* spp. tend to spawn during midmorning, and speculated that spawning in nature may be restricted by the fact that suitable spawning substrates are covered by high tide during midmorning only at fortnightly intervals. Correspondingly, a lacustrine population of *M. beryllina* spawns daily at midmorning (Hubbs 1976). Hence, in the laboratory where tidal cues are removed, spawning substrates are continuously available, and food is abundant, *M. menidia* responded by spawning more frequently. The high egg production of female A also suggests that if the supply of recruitment eggs is exhausted, new recruitment eggs can be formed. It is clear that estimates of fecundity in natural populations of multiple spawners based on laboratory studies alone should be interpreted with caution.

Many aspects of the fecundity and spawning periodicity of *M. menidia* are paralleled in a west coast atherinid, *Leuresthes tenuis*. The California grunion has a well-known semilunar spawning cycle (Walker 1952). Clark (1925) conducted a detailed study of egg diameter frequencies in ovaries of *L. tenuis* and concluded that each female spawns once about every 15 d. Batch fecundity was very similar to that reported here for *M. menidia*. Although Clark measured batch fecundity in only a few individuals, a 118 mm grunion contained 1,613 ova. I calculate that a 118 mm Atlantic silverside would be expected to have 1,704 ripening eggs during the middle of the breeding season. Clark also found retention of recruitment eggs at the end of the breeding season and presented histological evidence that retained eggs were being resorbed.

Based on my estimate of the average annual fecundity of *M. menidia* (893 ± 197 eggs/g ovary-free body weight) and the wet weight of ripe eggs (0.8 g/1,000 eggs), an Atlantic silverside produces nearly 0.7 of its body weight in eggs during the breeding season in nature. In the laboratory, females produced 1.1-2.7 times their body weight in eggs. Studies of other multiple spawners have yielded similar results. DeMartini and Fountain (1981) estimated that the queenfish could spawn about 114% of its body weight in a year. Experiments on several species of cyprinids indicate that they are capable of spawning 0.7 to 6.8 times the volume of the female in eggs, at least in the laboratory (Gale and Gale 1977; Gale and Buynak 1978, 1982; Gale 1983). Hubbs (1976) estimated that a freshwater population of *Menidia beryllina* spawned 6-8 times female weight in eggs, although his assumption that each female spawns daily throughout the length of the breeding season needs further documentation.

Subseasonal trends in batch fecundity among multiple spawners have been examined by few investigators. If trends in batch fecundity within the breeding season are the adaptive result of natural selection, then periods of maximum batch fecundity should reflect the period when the probability of offspring survival is greatest. On the other hand, trends in batch fecundity could simply result from varying food conditions for adults. Three general relationships between the batch fecundity and the time of the breeding season have emerged from field studies with which I am familiar. These include 1) constant batch fecundity during the breeding season (Fig. 6, curve A), 2) a concave downward relation between batch fecundity and the breeding season (Fig. 6, curve B), and 3) a constant decline in batch fecundity during the breeding season (Fig. 6, curve C). Constant fecundity (curve A) might be expected where the optimal environmental conditions for reproduction and offspring survival are constant or vary unpredictably during the breeding season. This pattern has been found in the queenfish (DeMartini and Fountain 1981), a pelagic spawner of the western North American coast where aperiodic upwelling events produce unpredictable variations in plankton productivity and potential larval survival (Lasker 1978). When seasonal environmental conditions change in a predictable manner, there may be an optimal period for reproduction that occurs at roughly the same time each year, and batch fecundity would be expected to be maximal at that time (curve B). In *M. menidia*, the relation between batch fecundity and the breeding season was concave downward, suggesting that reproductive success is maximal during the middle of the breeding season. There is some independent evidence to support this hypothesis. Winter mortality during the offshore migration is

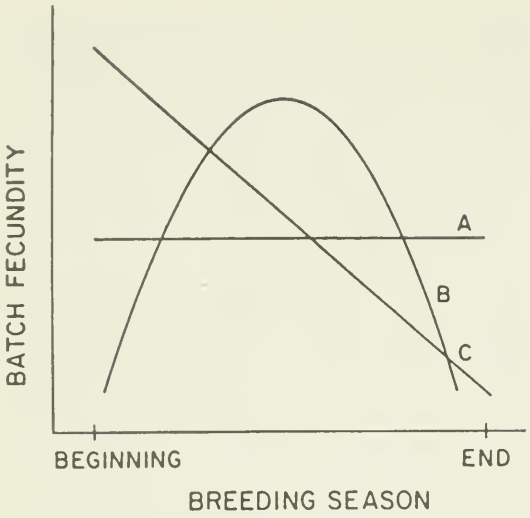

FIGURE 6.—Three hypothetical relationships between batch fecundity and time of the breeding season that have empirical support in the literature. A) Constant batch fecundity. B) Batch fecundity maximal during the middle of the breeding season. C) Batch fecundity maximal at the beginning of the breeding season and declining continuously thereafter.

strongly size-selective in *M. menidia* (Conover and Ross 1982; Conover 1984): the largest young-of-the-year have the highest probability of surviving. Hence, there should be selection pressure to breed as early in the spring as physical conditions (such as temperature) permit, and perhaps before conditions are optimal. Any offspring that managed to survive early in the breeding season will ultimately benefit from having a longer growing season. Conversely, towards the end of the breeding season, energy placed into reproduction becomes wasted because these offspring will have almost no chance of growing to a size that will permit winter survival. It follows that somewhere in the middle of the breeding season will be the optimal period for reproduction. Declining batch fecundity during the breeding season (curve C) has been reported for a population of the common mummichog, *Fundulus heteroclitus*, where batch fecundity was greatest at the beginning of the breeding season and became progressively less thereafter (Kneib and Stiven 1978). A continuous decline in batch fecundity may evolve when the value of putting energy into current reproduction, as opposed to somatic growth, declines continuously as the breeding season progresses. Although few data are now available for comparing the subseasonal patterns of batch fecundity in multiple spawning fishes, such information may eventually prove useful in understanding the general reproductive strategies of fishes.

ACKNOWLEDGMENTS

I thank the staff of the University of Massachusetts Marine Station for logistic support. D. Chevalier assisted in maintaining the laboratory fish and in counting eggs. F. Sutter helped with field sampling. The comments of two anonymous reviewers improved the clarity of the manuscript. During part of the this study, I received support from the Massachusetts Cooperative Fishery Research Unit, which is jointly funded by the Massachusetts Division of Marine Fisheries, the Massachusetts Division of Fish and Wildlife, the University of Massachusetts, and the U.S. Fish and Wildlife Service.

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PARASITES OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*: FISHERY IMPLICATIONS

R. J. G. Lester,[1] A. Barnes,[2] and G. Habib[3]

ABSTRACT

The numbers of 26 types of parasites were counted in 878 fish, of which all but 3 were from 14 areas in the Pacific. Data from the 22 most reliable parasites gave no evidence of discrete stocks of skipjack tuna in the Pacific, either when analyzed singly or when using combinations of parasites in multivariate analyses. New Zealand fish carried many tropical parasites, particularly didymozoids, in numbers similar to fish caught in the tropics, indicating that the bulk of these fish had recently migrated from the tropics. The number of *Tentacularia coryphaenae*, a larval tapeworm, was positively correlated to fish size in the tropics. In New Zealand, however, fish over 55 cm carried about the same number of *T. coryphaenae* as fish 45 to 55 cm, suggesting they had left the tropics when they were 45 to 55 cm and had not returned.

Analysis of the numbers of parasites from particular schools suggested that school members stayed together for several weeks but not for life.

The use of parasites to delineate stocks for management purposes is a well-established technique. For a comprehensive review of the many examples see MacKenzie (1983).

The skipjack tuna, *Katsuwonus pelamis*, is one of the most valuable fishery resources of the central and western Pacific. At least 50 species of parasites have been reported from it. The distribution of only one, the hemiuroid digenean *Hirudinella ventricosa*, has previously been investigated. In the Atlantic, Watertor (1973) found it in 7% of skipjack tuna off West Africa, 40% off Brazil, and < 1% off Florida. In the Pacific, Nakamura and Yuen (1961) found it in 21% of skipjack tuna off the Marquesas and 34% of fish from Hawaii. Sindermann (1961) pointed out that analyzing the distributions of combinations of parasites may provide more information than the examination of individual species. That, in general, has been our approach here.

In addition, school-school variation in parasite numbers was studied to determine how long schools stayed together, and secondarily to evaluate the degree of permanence of the parasites.

MATERIALS AND METHODS

Of the 878 fish dissected, 386 were collected by the *Hatsutori Maru* on charter to the South Pacific Commission (SPC), 246 by the New Zealand Ministry of Agriculture and Fisheries (NZ), and the remainder by other governments and fishing companies (see Acknowledgments). Fish were obtained from 15 areas (Fig. 1, Table 1).

Gills and viscera were frozen and flown to Brisbane for dissection. The SPC and NZ fisheries officers sampled 5 fish/school from a maximum of 3 schools/d. Commercial companies were unable to sample from individual schools and usually supplied the head and the anterior ventral body, removed from frozen fish by a single slanting cut using a band saw. Fork length, if not supplied, was calculated

TABLE 1.—Sources of fish dissected.

	Area	Date	No. fish	Avg. length (cm)
A	Palau, Helen R.	Aug. 1980	35	41
B	Ponape	July 1980	45	59
C	Papua New Guinea	June 1981	30	50
D	Papua New Guinea	Nov. 1981	60	41
E	Solomon Is.	June 1980	30	46
F	Coral Sea	Jan. 1982	19	57
G	Fiji	Feb., Mar., Apr., May 1980	100	50
H	Norfolk Is.	Mar. 1980	21	57
I	New South Wales	Jan. 1981	103	47
J	New Zealand, west	Mar. 1980; Jan., Feb. 1982	69	52
K	New Zealand, east	Jan. 1980; Jan., Feb. 1982	163	49
L	Marquesas	Dec. 1979; Jan. 1980	150	47
M	California	Aug. 1981	30	47
N	Ecuador	Jan. 1982	20	48
O	Atlantic (Puerto Rico)	Mar. 1981	3	50

[1]Department of Parasitology, University of Queensland, St. Lucia, Brisbane, Australia 4067.
[2]Faculty of Science, University of Queensland, St. Lucia, Brisbane, Australia 4067.
[3]Fisheries Research Division, New Zealand; present address: Southpac Fisheries Consultants, P.O. Box 7230, Auckland 1, New Zealand.

Manuscript accepted November 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

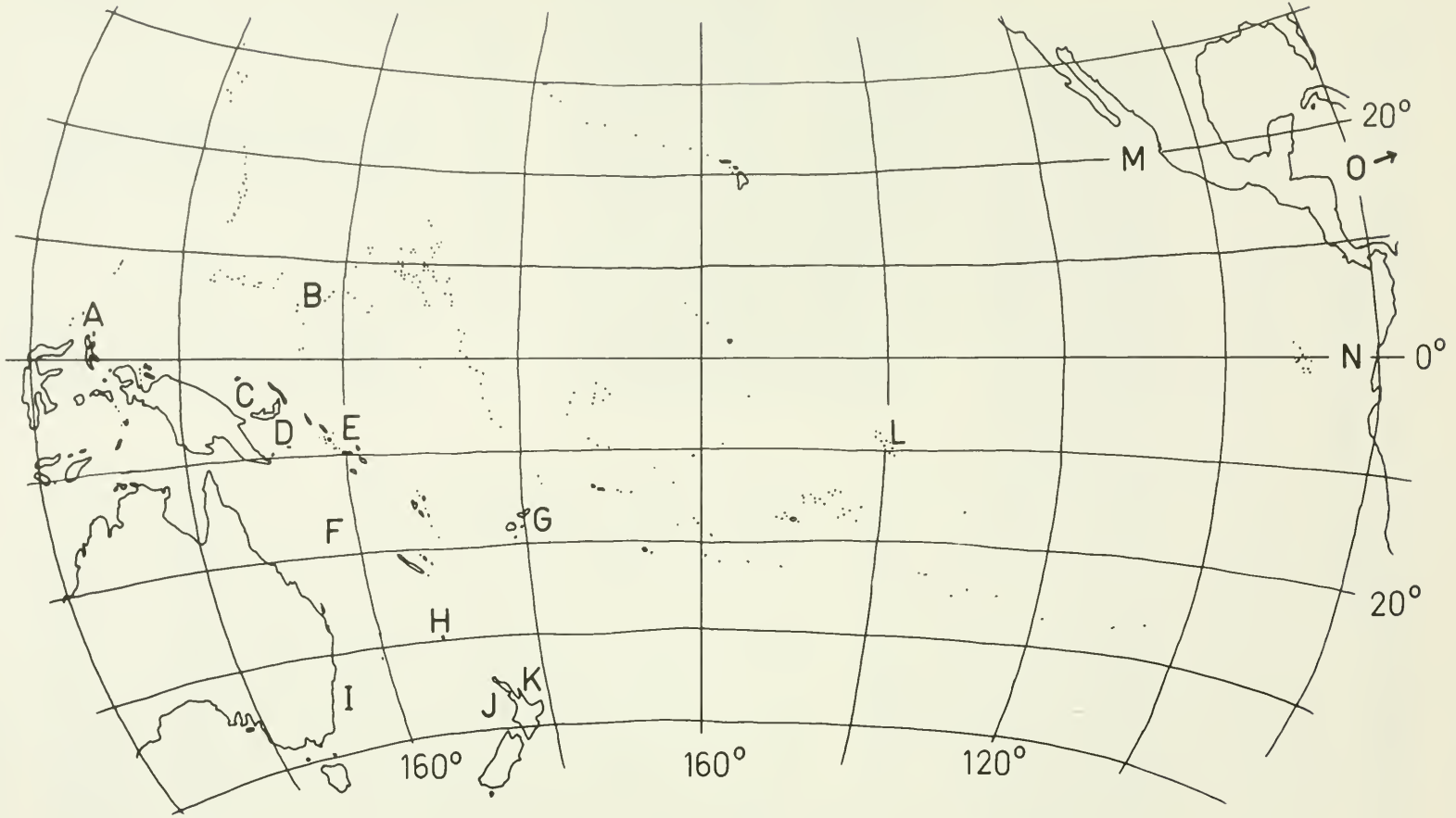

FIGURE 1.—The 15 sites, A to O, from which fish were received for parasitological analysis. A = Palau, Helen Reef; B = Panape; C and D = Papua New Guinea; E = Solomon Islands; F = Coral Sea; G = Fiji; H = Norfolk Island; I = New South Wales; J = New Zealand West; K = New Zealand East; L = Marquesas Islands; M = California; N = Ecuador; O = Atlantic (Puerto Rico).

from head length using the formula 7.8 + 2.75 × (head length) for heads under 14.5 cm and −1.7 + 3.3 × (head length) for larger heads (from measurements of 80 and 83 fish, respectively). Prior to dissection, fish were thawed overnight at 6°C. In general, all viscera parasites were counted whereas gill parasites were counted on one side only and the numbers doubled in the final tables. A didymozoid capsule was counted as one parasite though most contained two individuals. Representative parasites were fixed and stored in 10% Formalin[4] except for nematodes which were fixed and stored in 70% alcohol.

An additional set of data on the abundance of the larval cestode *Tentacularia coryphaenae* was collected at sea by SPC and NZ fisheries officers. They recorded the number of *Tentacularia* visible through the peritoneum in the wall of the body cavity of 1,529 fish.

Besides some summary statistics, two types of statistical analysis were done: 1) investigation into the similarities and dissimilarities of the parasite fauna between the various areas sampled, and 2) a study of school integrity.

The similarities and dissimilarities between areas were examined using a series of cluster analyses and multivariate canonical analyses (Mardia et al. 1979). Strictly speaking, canonical analyses require data which are normally distributed and which have a common variance. However, the frequency distributions of the parasites were not normal. They showed considerable differences from one parasite to another and most appeared to have two components: one which could be adequately approximated by a negative binomial distribution; and a second component consisting of a disproportionately large zero category, presumably arising because some schools had not been exposed to infection. Precise transformations to normalize the data would thus have been complex and of doubtful accuracy considering the small size of the samples from each school. A single transformation for all species was therefore used: the natural logarithm of the number of parasites plus 1.0.

To avoid possible biases due to associations between parasite numbers and fish length, such as that shown in Figure 2, the transformed counts were then adjusted for fish length. This was done for each species by regressing log (parasite number + 1.0) on fish length, for all Pacific tropical fish (489), to estimate the magnitude of any relationship. This was used to adjust the transformed parasite numbers, except where this was zero, to that expected for a fish of a standard length of 50 cm. (This length was very close to the overall mean length of the fish.) The method could not be trusted to eliminate all effects of length, so, as an added safeguard, only fish 39.5 to 57.5 cm were used in the multivariate analyses (83% of the total). These are likely to have been 1 yr old (Uchiyama and Struhsaker 1981; Wankowski 1981).

In a few instances a parasite was absent from all fish in one area. To allow matrix inversion in the canonical variate analyses, a random number between −0.005 and +0.005 was added to the data. This did not influence the outcome. The results of the canonical variate analyses were displayed graphically as plots of the first versus the second canonical

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

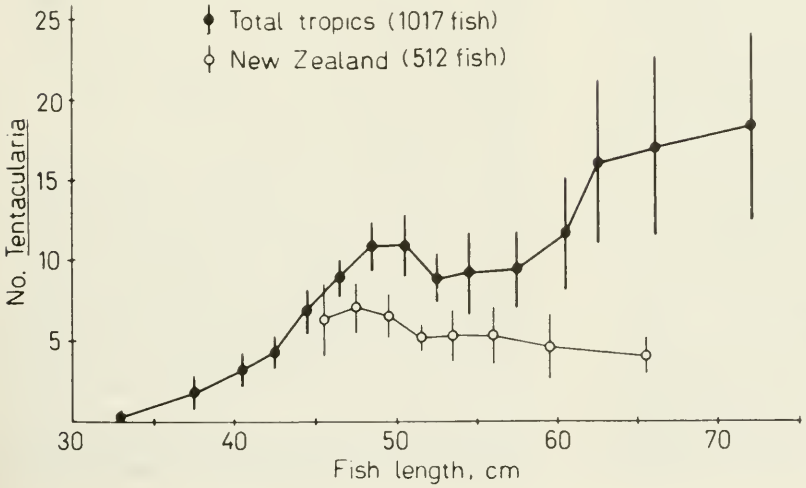

FIGURE 2.—Relationship between number of *T. coryphaenae* and fish length. Mean ±2 SE. Each mean from minimum of 19 fish. In the tropics the number increased with length but this was not reflected in the New Zealand samples.

axes. Confidence limits (95%) for the positions of different areas on these plots are presented as circles with radius equal to the square root of 5.99/number of fish in sample (Mardia et al. 1979).

Analyses on the same combinations of parasites were also done by calculating minimum spanning trees (Gower and Digby 1981), and dendrograms from nearest neighbor and centroid cluster analyses (Clifford and Stephenson 1975), basing similarity measures on logarithms of area means. Areas were grouped in a similar way by all methods. Using clustering algorithms which either ignored or allowed for matches between areas where parasites were not recorded did not significantly influence results. For these reasons, and because only canonical variate analysis provided some measure of reliability for its conclusions (confidence rings), only the results of the canonical analyses are presented below.

School integrity was examined by comparing the variability in parasite numbers per fish between schools, to that within schools, for the two areas (Marquesas and east New Zealand) where the largest numbers of schools were sampled. This showed which parasites were strongly linked to schools, and also allowed tentative estimation of the length of time schools remained intact. In theory, for parasites to show strong school associations two conditions need to be met: the parasite must heavily infect some schools and not others, and its life span in the fish must be equal to or shorter than the life of the school. Parasites which showed strong school-school association were therefore likely to be shorter lived than those not showing such associations, and other evidence being equal, were considered less reliable as population markers than related species.

Two methods were used to compare within and between school variability in each of the two areas. First, a series of univariate analyses of variance of log (parasite numbers + 1.0) were done to calculate the ratio of between school to within school variances. The magnitude of these ratios, and the corresponding probabilities that they do not differ from 1.0, were interpreted as measures of school integrity. A limitation of this method was that the data were only approximately normally distributed, particularly for rare parasites, and thus the derived probabilities were also approximations.

The second method, a median test, was based on the binomial distribution. The number of parasites of a particular species in each fish was transformed to a zero if it was less than or equal to the median number per fish for the area, and to a one otherwise. The zeros and ones of each school were then considered as a binomial sample. If these samples showed evidence of greater variation than expected by chance (i.e., too many schools with nearly all zeros or nearly all ones), then the schools differed with respect to the distribution of the parasite. A statistic, approximately distributed as a χ^2 random variable, was calculated using GLIM (Baker and Nelder 1978) to determine whether the binomial samples showed evidence of differences. Its associated probability was used as a measure of school integrity. The method had the useful property of being independent of the distribution of parasite numbers. For parasites with a median per fish of <1, the test was based on the presence or absence of the parasite, though obviously the rarer the parasite the less sensitive the test.

It is possible that some schools were sampled twice. If this did happen, the results of both methods err on the conservative side. Only those species that gave consistent results by both methods were used to draw conclusions about school integrity.

RESULTS

Evaluation of Parasite Species

Information was collected on 26 different types of parasites (species or species complexes) from 15 areas. A summary of the raw data unadjusted for fish length is given in Table 2.

The parasite species were evaluated for their probable longevity on or in skipjack tuna. For them to be useful as markers they needed to be relatively long-lived, preferably surviving for the life of the fish. Nothing was known specifically about their longevity in skipjack tuna, though data were available on related forms (Table 3). In general, intestinal lumen dwellers appear to be more easily lost than larval forms encapsulated in the tissues. The 26 skipjack tuna parasites were divided into four groups, those considered "temporary", "semi-permanent", and "permanent", and those not used at all.

Four parasites were not used in any analyses. Two of the nematodes, *Ctenascarophis* sp. and *Spinitectus* sp. (Nos. 23 and 24 in Table 2), were found in the gut of virtually every fish in which they were sought, from every area. Their small size meant that the number recovered was a function of the time spent searching. They were only counted in every fifth fish, as were the two larval cestodes from the large intestine, *Scolex polymorphus* (large) and *S. polymorphus* (small) (Nos. 25 and 26). Counting these was time consuming, their apparent abundance may have been inversely related to the state of preservation of

TABLE 2.—Average numbers of parasites per fish in all skipjack tuna (878) from the areas listed in Table 1, unadjusted for length. The last column gives the correlation coefficient (*r*) for length against log (parasite number + 1) for Pacific tropical fish.

No.	Parasites	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	*r*
1	*Caligus* spp.	5	17	5	5	10	36	4	3	3	3	1	7	0	1	7	0.37
2	*Didymocylindrus filiformis*	16	5	2	3	4	4	7	3	6	8	10	4	4	3	10	−0.14
3	*Didymocylindrus simplex*	16	7	4	6	13	11	14	12	18	26	18	14	15	6	3	−0.08
4	*Didymoproblema fusiforme*	4	1	0	1	1	1	4	1	4	2	3	3	3	1	1	−0.06
5	*Lobatozoum multisacculatum*	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.1	0.4	0.2	0.3	0.1	0.0	0.03
6	*Syncoelium filiferum*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	13.1	0.0	0.0	0.0	0.0	0.0	0.0	—
7	*Philometra* sp.	1	3	4	29	5	P[1]	2	2	3	3	1	6	6	1	8	0.02
8	*Anisakis* type I	1.0	0.2	2.7	1.0	0.7	1.6	0.2	0.5	0.9	2.1	1.5	0.6	0.2	0.1	2.7	0.13
9	*Anisakis* type II	0.2	0.0	0.0	0.1	0.0	0.1	0.0	0.4	0.1	0.8	0.2	0.0	0.4	1.2	2.3	−0.02
10	*Terranova* sp.	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.06
11	*Coeliodidymocystis* sp.	1.3	2.1	0.3	0.2	0.9	0.2	1.2	0.5	0.3	0.7	1.3	0.8	0.1	0.7	0.0	0.03
12	*Tentacularia coryphaenae*	3	22	P[1]	3	4	19	8	6	4	5	6	10	3	P[1]	P[1]	0.48
13	*Oesophagocystis dissimilis*	12	6	8	7	8	12	9	3	6	3	9	8	8	9	11	−0.05
14	*Kollikeria* / *Didymocystis* spp.	13	4	1	5	9	4	7	7	8	4	5	6	11	5	6	−0.11
15	*Dinurus euthynni*	55	9	19	35	66	1	2	3	0	0	0	15	0	0	0	−0.34
16	*Didymocystoides intestino-muscularis*[2]	30	27	26	37	49	39	54	18	15	12	16	44	134	17	64	−0.14
17	*Hirudinella ventricosa*	0.4	0.6	0.4	0.2	1.1	0.7	0.4	0.3	0.1	0.0	0.0	1.1	0.1	0.2	1.0	−0.10
18	*Raorhynchus terebra*	22	16	13	17	15	18	25	65	4	2	4	12	3	1	0	−0.00
19	*Didymocystoides intestino-muscularis*[2]	14	3	3	9	3	8	5	8	6	6	6	7	13	3	2	−0.24
20	*Lagenocystis* / *Univitellannulocystis* spp.	76	40	29	29	22	45	43	16	38	17	30	61	178	34	41	−0.11
21	*Tergestia laticollis*	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.8	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.00
22	*Rhipidocotyle* sp.	0.0	0.3	0.0	0.2	0.2	2.3	2.4	0.0	1.3	0.0	0.0	0.1	0.0	0.0	0.0	0.08
23	*Ctenascarophis* type	35	7	6	2	18	22	38	49	7	17	21	33	4	1	108	
24	*Spinitectus* type	10	7	20	2	12	5	9	10	5	6	18	13	5	3	10	
25	*Scolex polymorphus* (large)	4	0.4	0.2	0	7	166	33	P[1]	122	101	27	10	161	9	7	
26	*Scolex polymorphus* (small)	200	124	1,089	287	8,900	257	463	140	211	53	24	206	495	153	105	

[1]P = present.
[2]No. 16—stomach; No. 19—intestine.

the fish, and their longevity was doubtful. *Philometra* sp. (No. 7) was found predominantly in developed ovaries, which were present in less than half of the fish sampled. The data were used for comparing school-school variability only.

Seven parasites were considered "temporary". They appeared to be short-lived or easily lost from the fish. The caligoid copepods (No. 1, primarily *Caligus productus* in the tropics and *C. bonito* in temperate waters) were not permanently attached and probably moved from fish to fish (Kabata 1981). *Syncoelium filiferum* (No. 6) was common on the gills in New South Wales and New Zealand samples (I, J, and K), but was not recovered from anywhere in the tropics. It is common on fish endemic to New Zealand (D. Blair[5]). It was considered possibly a temperate short-lived parasite, at least on skipjack tuna, and this was verified by the school integrity study and by conventional tagging data (see later).

Some hemiurids are known to be readily lost from the gut of other species of fish (Table 3). Margolis and Boyce (1969) observed that over half the *Lecithaster gibbosus* were lost from salmon fingerlings within 3 wk of bringing the fish into captivity. We found *Dinurus euthynni* (No. 15) in all tropical samples from the central and western Pacific but not in the temperate samples I, J, and K. As it showed strong school associations and as the didymozoid data described later showed that New Zealand fish had a recent origin in the tropics, *D. euthynni* was evidently a short-lived tropical parasite that was lost as the fish migrated south. This also appeared to be true for *Hirudinella ventricosa* (No. 17) and possibly for two relatively rare gut-lumen digeneans, *Tergestia laticollis* (No. 21) and *Rhipidocotyle* sp. (No. 22).

In other fish, adult acanthocephalans may be short lived (Table 3). Möller (1976) found that over half the *Echinorhynchus gadi* in three species of fish were lost within 2 wk of the fish being brought into captivity. In our data, *Raorhynchus terebra* (No. 18) was present in reduced numbers in I, J, and K, suggesting it was lost in southern waters. All these parasites then were labelled "temporary".

Didymozoid digeneans were considered "semi-permanent" parasites. In other fish, some didymozoids, or at least the remains of them, are believed to stay in the tissues for the life of the fish. Others, including some species found in the gonads or gills, are lost annually (Table 3). In general, therefore, skip-

[5]D. Blair, Department of Zoology, University of Canterbury, Christchurch, New Zealand, pers. commun. September 1984.

TABLE 3.—Probable maximum life spans of parasites related to those found in skipjack tuna.

Parasite	Site	Host	Life span	Reference
Acanthocephala				
Echinorhynchus gadi	Intestine	*Zoarces viviparous*	2 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Gadus morhua*	6 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Myxocephalus scorpius*	7 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Platichthys flesus*	11 wk	Moller (1976)
Acanthocephalan sp.	Intestine	*Sparus aurata*	< 8 wk	Paperna et al. (1977)
Hemiurid Digenea				
Lecithaster gibbosus	Int. and caec.	*Oncorhynchus gorbuscha*	< 9 mo	Boyce (1969)
Lecithaster gibbosus	Int. and caec.	*Oncorhynchus gorbuscha*	> 5 mo	Margolis and Boyce (1969)
Lecithaster gibbosus	Int. and caec.	*O. keta*	8 mo	Margolis and Boyce (1969)
Tubulovesicula lindbergi	Stomach	*O. keta*	> 31 mo	Margolis and Boyce (1969)
Lecithophyllum botryophorum	Stomach	*Argentina silus*	10 mo	Scott (1969)
Didymozoid Digenea				
Nematobothrium texomense	Ovary	*Ictiobus bubalus*	> 8 mo	Self et al. (1963)
Neometadidymozoon helicis	Buc. cav.	*Platycephalus fuscus*	1 yr	Lester (1980)
Nematobothrium spinneri (eggs)	Muscle	*Acanthocybium solandri*	> host	Lester (1980)
Larval Cestoda				
Gilquinia erinaceus	Mesentery	*Melanogrammus aeglefinus*	> host	Lubieniecki (1976)
Trypanorhynch sp.	Mesentery	*Clupea harengus*	> 1 yr	Sindermann (1961)
Triaenophorus crassus	Mesentery	*Oncorhynchus* spp.	> host	Margolis (1965)
Larval Anisakinae				
Larval anisakid	Mesentery	*Clupea harengus*	> 1 yr	Sindermann (1961)
Larval anisakid	Mesentery	marine fish	several years	Margolis (1970)
Porrocaecum decipiens	Mesentery	*Gadus morhua*	several years	Platt (1976)

jack tuna didymozoids were thought to be in the fish probably for at least several months. However, there was some suggestion that 3 of the 10 skipjack tuna didymozoids had a shorter adult life span than the others. Didymozoid No. 16 was much less common in New Zealand waters than in the tropics (Table 4), and didymozoid Nos. 19 and 20 were also less common and, in addition, showed strong school associations (see later). These three didymozoids (possibly representing four species) were omitted from the analysis for Figure 3.

The remaining four parasites (Nos. 8, 9, 10, and 12) were classed as "permanent". Larval cestodes and nematodes, particularly those found in the tissues, are generally believed to survive for several years, often for the life of the fish (Table 3). They have been used successfully many times as fish population markers (see MacKenzie 1983). In skipjack tuna, the larva of a trypanorhynch cestode, *Tentacularia coryphaenae*, was found in the wall of the body cavity and occasionally in the viscera. No degenerating forms were seen, suggesting that it survived for an extended period and hence could be an excellent population marker, though counts were not available from areas C, N, and O. Larval anisakids were found on the wall of the stomach or in the mesentery. The literature suggested that they should also be good long-term markers (Table 3). They were counted in all areas.

Protozoan parasites have been used successfully to separate stocks of several species of fish. However, none has been reported from skipjack tuna, and we found none in this study.

TABLE 4.—Average number of didymozoids in New Zealand fish (all lengths) compared with fish caught in the tropical western Pacific (areas A, B, C, D, E, F, G, and L). In parentheses, log $(x + 1)$ length-adjusted means for fish 40 to 57 cm only.

No.[1]	Parasite	New Zealand		Tropics	
2	*D. filiformis*	9	(1.1)	6	(0.8)
3	*D. simplex*	20	(1.7)	12	(1.3)
4	*D. fusiforme*	2.7	(0.6)	2.5	(0.5)
5	*L. multisacculatum*	0.3	(0.1)	0.1	(0.0)
11	*Coeliodidymocystis* sp.	1.1	(0.4)	0.9	(0.3)
13	*O. dissimilis*	7	(1.3)	9	(1.9)
14	*Kollikeria* / *Didymocystis* spp.	5	(1.2)	6	(1.5)
16	*D. intestinomuscularis*[2]	15	(1.8)	41	(3.3)
19	*D. intestinomuscularis*[3]	6	(1.3)	7	(1.4)
20	*L. katsuwoni* / *U. katsuwoni*	26	(1.9)	47	(2.3)
	No. of fish	232	(213)	469	(364)

[1]Code no. from Table 2.
[2]Stomach.
[3]Intestine.

Relationships Between Areas

Analyses of individual distributions of permanent and semipermanent parasites showed that the abundances of individual parasites varied across the Pacific. However, these differences were inconsistent, the pattern established by one parasite being in conflict with that of a second, and so on.

The data from the three anisakid nematodes and the seven didymozoids considered longest lived were therefore analyzed using canonical variate analysis. Because of the more permanent nature of these parasites and the completeness with which they were recorded from all areas, these data were considered the most reliable for statistically assessing the similarities and dissimilarities between areas. The first three canonical axes accounted for 75% of the

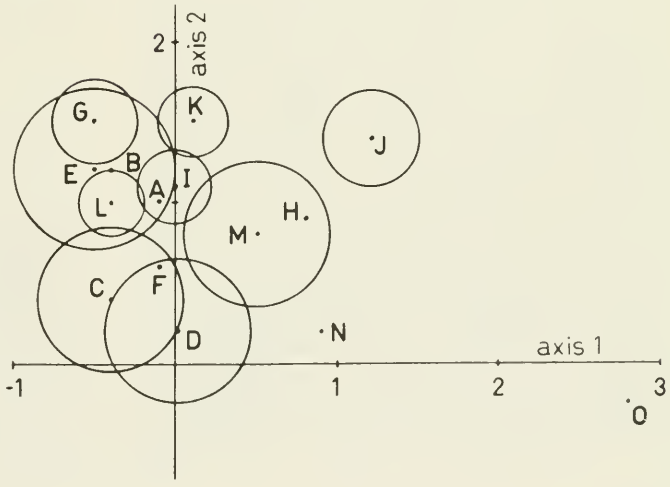

FIGURE 3.—Results of multivariate analysis using 3 "permanent" and 7 "semipermanent" parasites (Nos. 2, 3, 5, 8, 9, 10, 11, 13, and 14). Values for first two canonical vectors plotted, and 95% confidence rings indicated for samples of more than 24 fish. The letters refer to the sampling sites indicated in Figure 1.

variation in area-to-area differences in parasite numbers. A plot of the first two, accounting for 58% of the variation, showed the Atlantic fish (O) to be distinct from all the Pacific ones, even though only three fish from the Atlantic were dissected (Fig. 3). However, fish from California (M) and Ecuador (N) fell close to the western Pacific samples. They were separated out on the third axis (not shown), but nevertheless it is evident that they had a somewhat similar parasite fauna. The fish from western New Zealand (J) appeared distinct, and so too, to a less extent, were the Papua New Guinea samples (C and D). There is no suggestion that fish from Ponape (A), Palau (B), Solomon Islands (E), Fiji (G), and the Marquesas (L) had distinct faunas of these long-lived parasites.

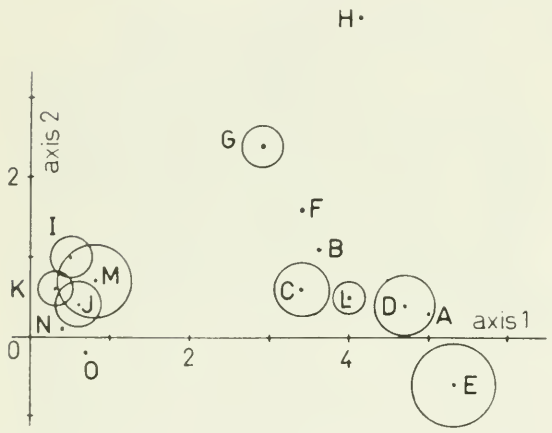

FIGURE 4.—Results of multivariate analyses using 7 "temporary" parasites (Nos. 1, 6, 15, 17, 18, 21, and 22). 95% confidence rings given for samples of more than 24 fish.

In this analysis, *Anisakis* II had the most powerful discriminating properties, though at least 7 of the 10 parasites used were capable of substantial discrimination in their own right.

An analysis based on the 7 "temporary" parasites (Nos. 1, 6, 15, 17, 18, 21, and 22) produced a much greater separation of areas (Fig. 4). They are grouped into two broad classes: one containing New South Wales (I), New Zealand (J, K), and the eastern Pacific (M, N); and the other the western tropical areas. Each area in the latter group had a temporary parasite fauna that was distinct from most other areas. Over 83% of the variation was accounted for by the first two axes, and 90% by the first three. It is interesting to note that New South Wales (I) is more similar to east New Zealand (K) than to west New Zealand (J) (this was much more marked on the third axis, not shown, where I and K were pulled to one side), and that west New Zealand is similar to California (M) and Ecuador (N).

Taken together, Figures 3 and 4 indicate that several distinct skipjack tuna parasite faunas existed within the tropical Pacific, and the longer lived parasites were more evenly distributed than the shorter lived ones.

To check these results and to look for links between the New Zealand fish and the tropical areas, the west Pacific data were reanalyzed using first the 10 "semipermanent" parasites (the didymozoids) and second the 4 "permanent" parasites (anisakids and *T. coryphaenae*).

The average numbers of didymozoids in the New Zealand fish were almost identical to the overall average for the central and western tropics (Table 4). In the multivariate analyses, the temperate water samples fell to one side of the tropical samples (Fig. 5

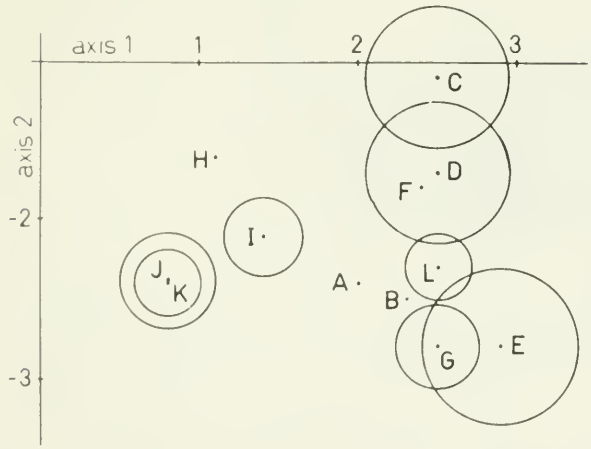

FIGURE 5.—Results of multivariate analysis using 10 didymozoids only (Nos. 2, 3, 4, 5, 11, 13, 14, 16, 19, and 20). 95% confidence rings given for samples of more than 24 fish.

–H, I, J, K), possibly because of the three didymozoids suspected of being relatively short-lived (Nos. 16, 19, and 20). The east and west New Zealand samples (J, K) were identical on the first two axes, and separated only slightly on the third axis (not shown). There was no obvious link between New Zealand and any particular tropical area.

Similarly, the larval nematodes and *T. coryphaenae* (Nos. 8, 9, 10, and 12) did not suggest a link between New Zealand fish and those from any particular tropical area (Fig. 6). However, west New Zealand (J) now appeared distinct from east New Zealand (K) and New South Wales (I). The separation was due to areas having either high *Anisakis* I and II and low *Terranova* and *T. coryphaenae* or low *Anisakis* I and II and high *Terranova* and *T. coryphaenae*. West New Zealand (J) was at one extreme (high *Anisakis*) and the three most northwestern areas–Ponape (B), Fiji (G), and Marquesas (L)–at the other. *Tentacularia coryphaenae* and probably *Terranova* were picked up in the tropics. It seems likely that one or both of the *Anisakis* larvae were picked up predominantly in temperate waters, particularly in west New Zealand. This may explain the separation of west New Zealand from the other areas in Figure 4.

In summary, the New Zealand fish were not closely aligned with any particular tropical sample, and the eastern and western New Zealand fish were probably carrying similar parasite faunas when they arrived in New Zealand.

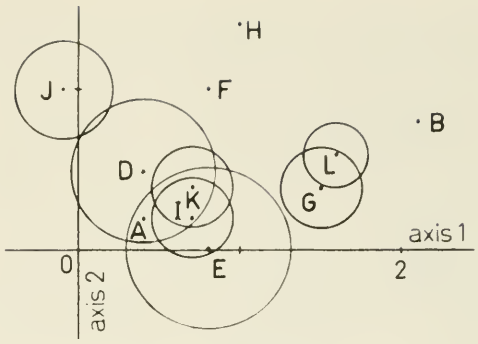

FIGURE 6.–Results of multivariate analysis using the four "permanent" parasites (anisakids and *T. coryphaenae*, Nos. 8, 9, 10, and 12). 95% confidence rings given for samples of more than 24 fish.

Tentacularia coryphaenae

Data on this parasite are presented in detail because we had more than for any other parasite and because potentially it was our most valuable marker. It also was the subject of many queries from skipjack tuna processors. The parasite was common throughout the south, central, and west Pacific (Table 3, parasite No. 12). The means of samples of over 22 fish within the length range 44 to 53.9 cm suggested an east-west cline across the Pacific, with twice as many parasites being found in fish from around the Marquesas (L) as around Papua New Guinea (C and D) (Fig. 7). A regression analysis of number of parasites against longitude using tropical data on the number of parasites in 972 fish, transformed and adjusted for differences in host length (data collected independently by the SPC), showed that the relationship was statistically significant, though it only accounted for about 7% of the fish-to-fish variation.

Considering fish of all sizes, the number of *T. coryphaenae* in the tropics increased with the size of the fish (Fig. 2, solid circles). The increase around 47 cm is due to many of the Marquesas fish being this size and Marquesas fish tended to have more *T. coryphaenae*. In New Zealand, smaller fish had about the same average number as fish from the tropics. However, this number did not increase with size (Fig. 2, open circles). Thus, the 58+ New Zealand fish had fewer parasites than their peers in the tropics, and about the same number as the 45 to 50 cm fish.

School-to-School Variation

An analysis of variance, and a median test, were carried out on 30 schools from the Marquesas and 19 schools from eastern New Zealand (areas L and K, respectively, Table 5). The results of the two methods on each data set show close agreement.

In the Marquesas, five parasites showed strong evidence of association with particular schools, i.e., the probability that schools differed was at least 0.95 with both methods. The parasites were *Caligus* spp. (No. 1), *D. euthynni* (No. 15), *H. ventricosa* (No. 17), *D. intestinomuscularis* (No. 19), and *Lagenocystis*/*Univitellannulocystis* spp. (No. 20). For these parasites to show significant differences, they must have heavily infected some schools and not others, and their life span in the fish must have been equal to or shorter than the life of the school. The literature review suggested that the first three species could possibly be readily lost from fish, and this is vindicated by their strong school association. The evident impermanence of the last two, however, was unexpected. It was as a consequence of this finding that they were not included in the analysis for Figure 3.

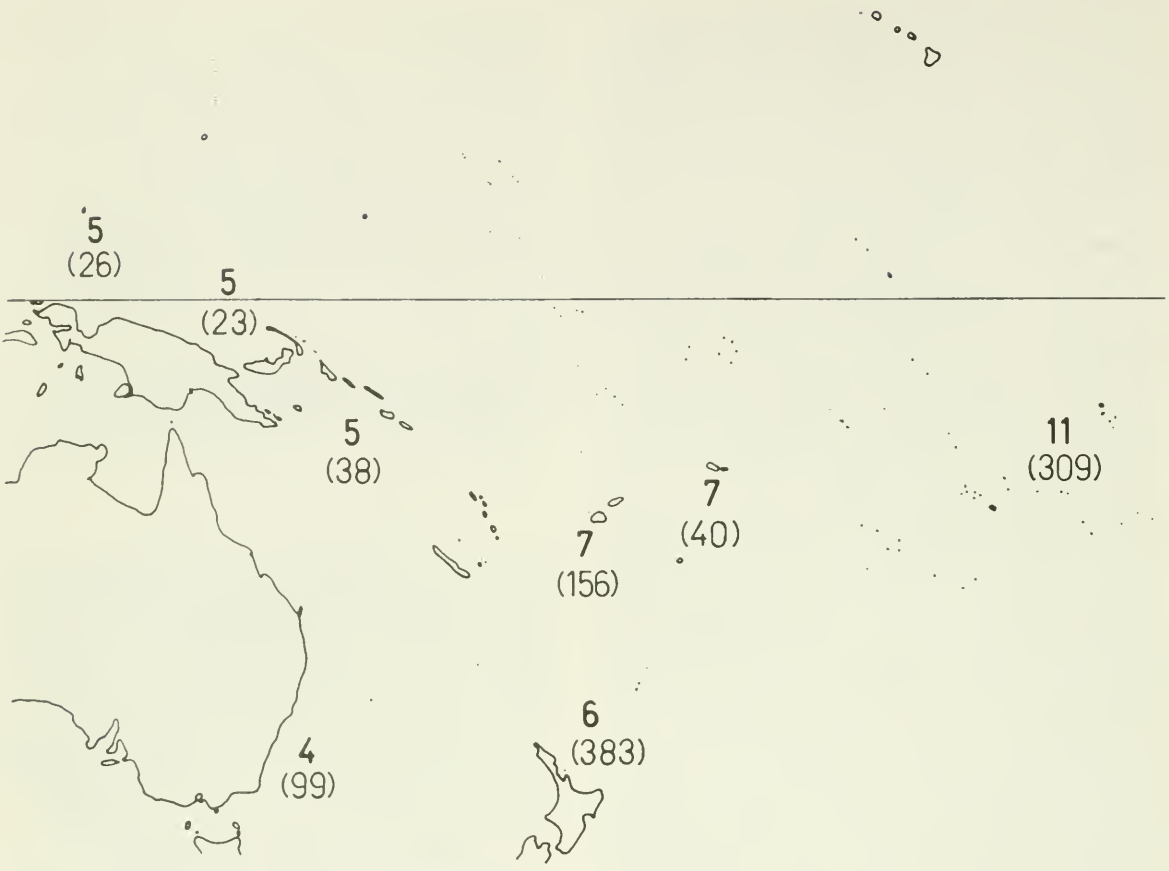

FIGURE 7.—The average numbers of *T. coryphaenae* in skipjack tuna 44 to 53.9 cm long in samples of over 22 fish. Note that the number increased to the east. (In parentheses, number of fish sampled.)

Several other parasites thought to be short-lived, such as *R. tereba*, did not show up in the test, presumably because their infective stages were relatively evenly distributed in the tropical Pacific.

In New Zealand, parasites showing close association with particular schools (using both tests) were *L. multisacculatum* (No. 5), *S. filiferum* (No. 6), *Philometra* sp. (No. 7), *Coeliodidymocystis* (No. 11), *T. coryphaenae* (No. 12), *R. terebra* (No. 18), and *D. intestinomuscularis* (No. 19). *Syncoelium filiferum* and *R. terebra* were both thought to be temporary parasites that could be gained in New Zealand or adjacent waters (Norfolk Island). The origin of the *Philometra* was unknown. Their number reflected the state of maturity of the fish and this varied between schools. However, we were left with three didymozoids and *T. coryphaenae*, all of which differed markedly between schools in eastern New Zealand. One of the didymozoids, *L. multisacculatum*, a normally rare tropical parasite, was found on all five fish from one school (numbers per fish 1, 2, 8, 3, and 1). As the three didymozoids and *T. coryphaenae* are essentially tropical parasites, the schools had evidently not fully mixed while in temperate waters.

If this is true, these four parasites could not have been picked up uniformly across the Pacific. Evidence is given above that *D. intestinomuscularis* (No. 19) was not picked up uniformly even within the Marquesas. For the other species, a comparison of their mean numbers per fish per school in different areas of the tropical Pacific showed that *Coeliodidymocystis* sp. and particularly *T. coryphaenae* were indeed more abundant in some areas than others. *Lobatozoum multisacculatum* was too rare for any conclusions to be drawn in this respect.

TABLE 5.—Comparison of within and between school variability in numbers of parasites per fish for two areas.

Parasite no. (see Table 3)	Marquesas		New Zealand	
	Analysis of variance[1]	Median test[2]	Analysis of variance	Median test
1	***[3]	***		
2		**		
3		*		
4				
5			***	**
6	(no parasites found)		***	***
7			*	*
8		*		
9				
10			(no parasites found)	
11			*	*
12			*	***
13				*
14				
15	***	**	(no parasites found)	
16				
17	*	*		
18			***	***
19	***	***	*	***
20	**	***		
21	*			
22				

[1]The probabilities that the ratio of the between and within school variances is no greater than one. (Based on transformed data, i.e., log (parasite no. + 1.0).)

[2]The probabilities that the proportion of fish with more than the area median is the same for all schools.

[3]*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; blank = $P > 0.05$.

Rate of Mixing of Schools

To estimate the rate of mixing of schools we needed to know the distribution of the parasites among schools before, and after, some known time interval. This we did not have for any of the Marquesas samples.

In New Zealand, however, some approximate calculations could be made because schools arrived from the tropics at different times. Sixteen of the 19 east New Zealand schools were of similar-sized fish and were all caught within 1 mo. These schools were divided into two groups: "early arrivals" and "recent arrivals". (This was done by ranking the schools using a combination of four parasites whose prevalences were positively correlated with each other, Nos. 16, 18, 19, and 20, and which were thought to be relatively short-lived parasites picked up in the tropics. Thus high numbers indicated a recently arrived school.) From catch data (Habib et al. 1980), we calculated that there was an average of 3 to 4 wk between the capture of 25% and 75% of the annual catch. This interval was taken as the approximate period between the arrival times of the early group and the recent group. If mixing was occurring, one would expect that the school-school differences for tropical parasites would be greater when the fish first arrived (the recent arrivals) than after they had been there for a few weeks (the early arrivals). However, this we could not demonstrate. Our sample sizes at this point were rather small (eight schools in each category), and in fact the reverse appeared to be the case, the early schools having a generally higher variability than the recent arrivals. This suggested that the early arrivals had come from several areas (and still had not fully mixed), whereas many of the later arrivals had perhaps come from one area.

DISCUSSION

Ten of the 26 parasites counted were species of didymozoid trematodes. These are almost exclusively a tropical group. Yamaguti (1970), for example, found 84 different species of didymozoid in fish around Hawaii. None were recorded in checklists of parasites from New Zealand (Hewitt and Hine 1972) or Canada (Margolis and Arthur 1979). Thus, although skipjack tuna are caught in both tropical and temperate waters, their didymozoid infections are evidently picked up primarily in the tropics.

Larval didymozoids have been found in small fish and in invertebrates. It is almost certain that the definitive host becomes infected by feeding on an infected intermediate host (Cable and Nahhas 1962; Nikolaeva 1965). In the tropics skipjack 40 to 60 cm in length feed largely on fish, squid, and stomatopods (Argue et al. 1983). In New Zealand, however, they feed almost exclusively on euphausids (Habib et al. 1980, 1981). This completely different diet in New Zealand, together with the fact that no endemic New Zealand fish are known to carry any didymozoids, lead us to the conclusion that few, if any, didymozoids are picked up in New Zealand waters.

The occurrence of 10 species of didymozoids in skipjack tuna caught in New Zealand, in numbers very similar to fish of the same size caught in the tropics, thus indicates that New Zealand and tropical fish were found until recently in a similar tropical environment. Almost certainly, the New Zealand fishery is based on fish that have recently migrated from the tropics, and not on fish recruited as postlarvae in temperate waters. This disagrees with tagging data which show that the bulk of New Zealand skipjack tuna of known origin were off New South Wales 10 mo earlier. However, the tagging inference is applicable to < 4% of the total New Zealand fish (Argue and Kearney 1983). Our conclusion is in agreement with Argue et al. (1983) who found no juvenile skipjack tuna in the stomachs of adults from

subtropical waters, though juveniles formed a significant component of the adult diet in the tropics.

The absence of degenerating *T. coryphaenae* and the positive correlation of parasite number and host length suggest that the parasite was long-lived and accumulated in the fish with age. The low numbers of *Tentacularia* in the 57+ cm fish caught in New Zealand indicate that these fish have had a different history from their peers in the tropics. The bulk of the skipjack tuna caught in New Zealand are 45 to 55 cm long. Less than 10% measure 60 cm or more (Habib et al. 1980, 1981). We have concluded above that the majority of New Zealand fish recently arrived from the tropics. The *T. coryphaenae* data indicate that the 57+ cm fish left the tropics at 45 to 55 cm long and have not returned. Evidently as fish age, they become less migratory. This was hypothesized by Kearney (1978).

Large fish were not necessarily permanent residents in New Zealand, however. Of 17 57+ cm fish on which full dissections were carried out, 2 were carrying the acanthocephalan *R. terebra*, a parasite thought to be relatively short-lived (see above) and not picked up in New Zealand. *Raorhynchus terebra* was common in fish from Norfolk Island (area H). Thus some of the large fish may have recently come from areas as far away as Norfolk Island.

The first two canonical variate analyses comparing all areas sampled suggested that fish 40 to 57 cm long had moved between areas and carried the longer lived parasites with them. Parasitologically, there was no evidence of more than one stock of skipjack tuna in the Pacific. Richardson (1983) observed an east-west cline in the gene frequency of two enzymes across the Pacific. From an analysis of 200 gene frequencies he proposed an "isolation by distance" model for skipjack tuna. In this, the degree of mixing of skipjack tuna genes was inversely proportional to the distance between the spawning areas. Tagging data have confirmed that there is some mixing of adult skipjack tuna in the central and western Pacific (Kleiber and Kearney 1983), though more than 95% of the tagged fish recovered during the SPC program were caught within 1,000 mi of their point of release (Kearney 1982).

Schools of skipjack tuna have been observed to break up when feeding (Forsberg 1980). This and observations from aircraft where schools have been seen to merge and later separate (Habib unpubl. obs.) have led to the hypothesis that skipjack tuna do not remain in a particular school for more than a day or so. Certainly the pattern of recovery of SPC tags suggested that tagged skipjack tuna underwent considerable mixing amongst schools soon after release (Argue and Kearney 1983). However, using Marquesas data we found that several parasites showed strong school associations, particularly didymozoid Nos. 19 and 20 (*D. intestinomuscularis* and *Lagenocystis/Univitellanulocystis* spp.). In another didymozoid, *Neometadidymozoon helicis* from the gills of *Platycephalus fuscus*, it takes up to a year for the worms to migrate through the tissues, pair up, mature, and die (Lester 1980). Though only a short migration is needed for didymozoids 19 and 20, as they are intestinal parasites, the worms are still likely to be in the skipjack tuna for a period of weeks. Thus, their strong association with particular schools suggests that school half-life is likely to be in terms of at least weeks rather than days.

In New Zealand, the large school-school differences observed in the numbers of *T. coryphaenae* and several other tropical parasites, especially in the early arrivals, indicate that at the time of catching, the New Zealand schools had not mixed sufficiently to mask their previously distinct tropical faunas.

Do schools remain intact for an extended period, perhaps for the life of the fish? Sharp (1978) found evidence of genetic similarity between individuals in core schools, suggesting that some members of the school were siblings. However, none of *L. multisacculatum*, *Coeliodidymocystis* sp., or *T. coryphaenae*, three long-lived parasites that showed significant school-school differences in New Zealand, showed any significant differences in the Marquesas. This suggests that within the probable long life of these parasites, fish caught in the Marquesas had changed schools and had thus obscured any patchiness in the distribution of the infective stages of the parasites. The parasitological data, then, do not support the hypothesis that fish stay in the same school for life.

ACKNOWLEDGMENTS

We are indebted to R. E. Kearney, A. W. Argue, and other officers of the Skipjack Program, South Pacific Commission, for much of our material, much of the *Tentacularia* data, and assistance in preparing this report. Other material was obtained with the help of David Bateman, Heinz Tuna Cannery, Eden, N.S.W.; Paul Dalzell, D.P.I. Fisheries Research, Kavieng, P.N.G.; Bernie Fink, Van Camp Sea Food Co., San Diego, CA; James Joseph, IATTC, La Jolla, CA; Ted Morgardo, Star-Kist PNG Pty. Ltd., Rabaul, P.N.G.; and Ronald Rinaldo, Southwest Fisheries Center, La Jolla, CA. Their cooperation is greatly appreciated.

Taxonomic assistance was rendered by David

Blair, Department of Zoology, University of Canterbury, N.Z.; Rod Bray, British Museum (N.H.), London, U.K.; and Arlene Jones, Commonwealth Institute of Parasitology, St. Albans, U.K. For help with the dissections we thank C. Boel, K. Couper, B. M. Heath, M. K. Jones, M. S. Kennedy, G. G. Lane, and A. G. West. K. MacKenzie, D.A.F., Scotland, kindly reviewed an earlier draft of the manuscript.

The project was supported by a grant to H. M. D. Hoyte, Department of Parasitology, University of Queensland, from the Nuffield Foundation, U.K.

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BEHAVIOR OF BOWHEAD WHALES, *BALAENA MYSTICETUS*, SUMMERING IN THE BEAUFORT SEA: A DESCRIPTION[1]

BERND WÜRSIG,[2] ELEANOR M. DORSEY,[3] MARK A. FRAKER,[4]
ROGER S. PAYNE,[3] AND W. JOHN RICHARDSON[5]

ABSTRACT

Behavior of bowhead whales summering in the Canadian Beaufort Sea was observed from an airplane and occasionally from shore during 1980-82, mainly during August. Behavior varied between years. In 1980, whales alternated periods of socializing with periods of feeding in several different ways: near the bottom (as evidenced by surfacing with mud), in the water column (suspected during long dives), and skim-feeding at the surface. In 1981, more time was spent apparently feeding in the water column, with some socializing and skim feeding. In 1982, almost all activity appeared to be feeding in the water column. In 1980, most whales studied were in water only 10-40 m deep. In 1981 they were farther from shore and in > 20 m depth, and in 1982 long (10-30 min) dives were common in depths of 40-600 m. Variability in distribution and behavior presumably was related to availability of prey.

Besides feeding and socializing, we saw sporadic bouts of aerial activity (breaches, tail slaps, etc.) and log play. During 1981 and 1982 we observed young-of-the-year calves apparently waiting at the surface while adults fed below. In 1982, two such lone calves played with debris in the water.

During near-surface skim feeding, whales often associated in V-shaped or echelon formations, with up to 14 animals staggered behind and to the side of each other, all moving in the same direction at the same speed, with mouths wide open. We hypothesize that such coordinated movement may increase the efficiency of feeding on concentrations of small invertebrates.

In recent years, much has been learned about behavior of several species of baleen whales (e.g., Payne 1983). Most long-term studies of whales have been carried out during winter, when social interactions, mating, and calving occur more often than feeding. Recently, however, detailed studies have been conducted in summer, when whales are primarily feeding (e.g., Dorsey 1983).

This paper describes the general behavior of bowhead whales, *Balaena mysticetus*, in the summers of 1980-82. A companion paper gives a quantitative description of the surfacing, respiration, and dive patterns (Würsig et al. 1984). This study was done to provide background data necessary to interpret observations of bowhead behavior in the presence of offshore industrial activities (Richardson et al. in press).

The Western Arctic population of bowheads winter in the Bering Sea, and migrate north and east to the eastern Beaufort Sea in spring. During summer (late June to early September), most are off northwestern Canada in Amundsen Gulf and the eastern part of the Beaufort Sea (Fig. 1). In the commercial whaling era in the 19th century, many bowheads apparently summered in the Chukchi and western Beaufort Seas off Alaska (Townsend 1935), but bowheads are no longer present in significant numbers off Alaska in summer (Dahlheim et al. 1980). The eastern Beaufort Sea is believed to be a major feeding area for bowheads (Fraker and Bockstoce 1980), but previous to 1980 there had been no comprehensive studies of bowheads in that area.

METHODS

Aerial Observations

We observed from a Britten-Norman[6] Islander aircraft based at Tuktoyaktuk (Fig. 1). The Islander has two piston engines, high wing configuration, and low

[1]This paper has been reviewed by the U.S. Minerals Management Service (MMS) and approved for publication. Approval does not signify that the contents necessarily reflect the views and policies of MMS, nor does mention of trade names or commercial products constitute MMS endorsement or recommendation for use.

[2]Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, CA 95039.

[3]New York Zoological Society, Weston Road, Lincoln, MA 01773; present address: Center for Long Term Research, Inc., Weston Road, Lincoln, MA 01773.

[4]LGL Ltd., Environmental Research Associates, 22 Fisher Street, King City, Ontario L0G 1K0, Canada; present address: Sohio Alaska Petroleum Co., Pouch 6-612, Anchorage, AK 99502.

[5]LGL Ltd., Environmental Research Associates, 22 Fisher Street, King City, Ontario L0G 1K0, Canada.

[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

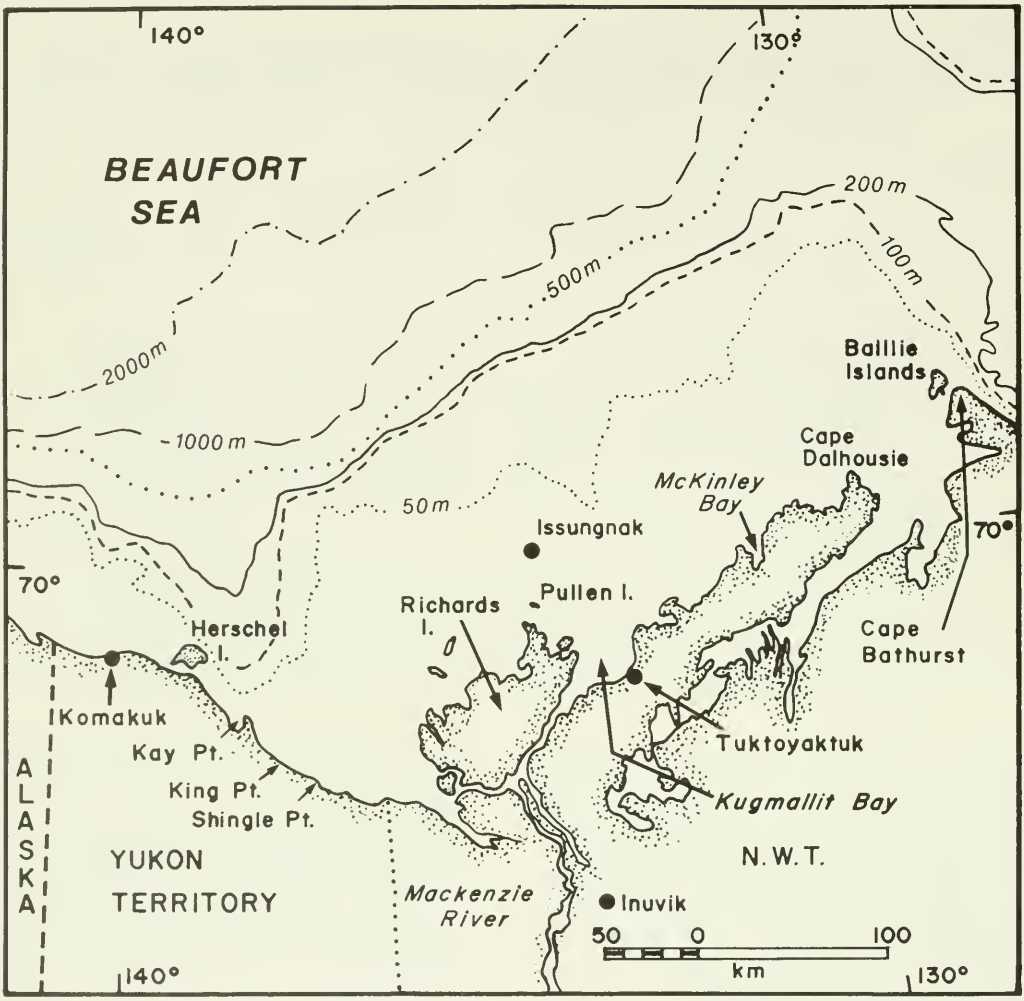

FIGURE 1.—The eastern Beaufort Sea.

stall speed. An OnTrac VLF/Omega navigation system indicated the latitude and longitude. A hand-held color video camera (JVC-CV-0001 in 1980 and 1981, Sony HVC-2000 in 1982) connected to a portable video cassette recorder (Sony SLO-340 in 1980 and 1981, Sony SL-2000 in 1982) was used through the side windows to record oblique views of bowheads.

Our usual strategy was to search until we encountered bowheads, and then circle over them as long as possible while making observations. If contact was lost, we searched for another group. We created a fixed reference point about which to circle when bowheads were below the surface by dropping a fluorescein dye marker. Near the start of most periods of circling above whales, a sonobuoy (AN/SSQ-41B or AN/SSQ-57A) was dropped to broadcast underwater sounds to the aircraft, where they were recorded.

In 1980-82, we flew for a total of 340 h during 71 offshore flights. Of this time, we circled over bowheads for 97.7 h during 46 flights. Flight duration was typically 4-5.5 h. Flights were made between 3 and 31 August 1980, 31 July and 8 September 1981, and 1 and 31 August 1982. We encountered bowhead whales during every day we flew in 1980, and during the majority of days in 1981 and 1982.

We usually did not fly when wind speed exceeded 25 km/h; in more severe conditions whales are difficult to detect and behavior cannot be observed reliably. While searching for whales, we usually flew at 457-610 m (1,500-2,000 ft) above sea level (ASL),

and at 185 km/h. While circling over whales, we reduced speed to 148 km/h. Bowheads rarely appeared to be disturbed by the aircraft when it remained at or above 457 m (Richardson et al. in press).

The aircraft crew usually consisted of four biologists and the pilot. Three biologists were seated on the right side of the aircraft, which circled clockwise during behavioral observations. Biologists seated in the right front (copilot's) seat and in the seat directly behind it described behaviors. These descriptions were recorded onto audiotape, onto the audio channel of the video recorder, and, in 1981, directly onto data sheets by a biologist in the left rear seat. The biologists in rear seats videotaped whales, handled sonobuoys, and kept records. All personnel on board were in constant communication through an intercom.

While circling bowheads, we usually were able to obtain consistent records of 12 variables and types of behavior:

1) Location of sighting (and, therefore, water depth);
2) Time of day;
3) Individually distinguishing features, if any, on whales;
4) Number of individuals visible in area and number of calves;
5) Headings and turns of each whale in degrees true;
6) Distances between individuals (estimated in whale lengths);
7) Length of time at surface, and sometimes length of dive;
8) Timing and number of respirations or blows, including underwater blows;
9) Possible indications of feeding: mouth open, defecation, mud streaming from mouth;
10) Socializing, possible mating, probable nursing by calves;
11) Aerial activity: breaches, tail slaps, flipper slaps, lunges, rolls;
12) Type of dive: flukes out, peduncle arch, predive flex.

Descriptions of these behaviors appear later.

In most parts of this paper we consider only the observations under "presumably undisturbed" conditions. Bowheads were considered "potentially disturbed" if our aircraft was at < 457 m ASL, if a boat was underway within 4 km, or if sonobuoys showed that industrial noise was readily detectable in the water. The "presumably undisturbed"

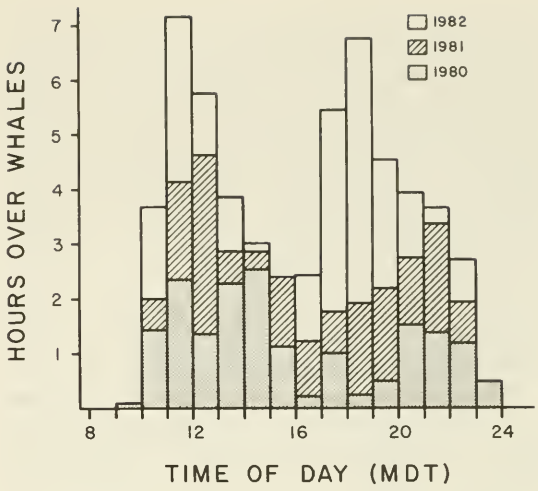

FIGURE 2. – Hourly distribution of behavioral observation time from the air of bowhead whales.

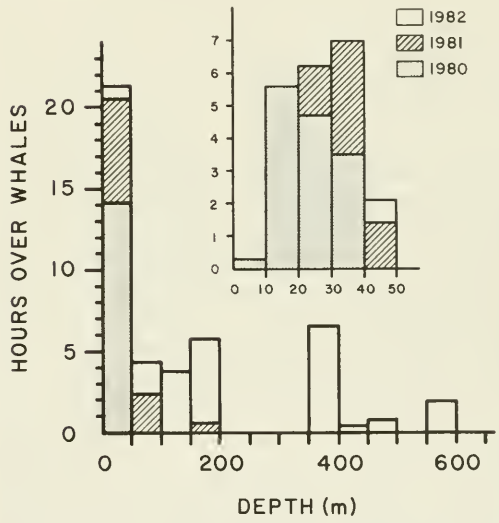

FIGURE 3. – Distribution of behavioral observation time from the air by depth of water of bowhead whales. The inset shows effort for the 0-50 m range by 10 m intervals.

behavioral observations were distributed by hour of day and water depth as presented in Figures 2 and 3.

Shore-Based Observations

Shore-based observations were obtained in 1980 and 1981 from the east end of Herschel Island, Yukon (lat. 69°35'N, long. 138°51'W), and about 225 km west of Tuktoyaktuk (Fig. 1). A surveyor's theodolite was used from a high point (50 m ASL in 1980,

90 m ASL in 1981) on the coast. We used a Wild T1 theodolite with 6-s accuracy and 30-power optics in 1980, and a Nikon NT-2A with 20-s accuracy and 30-power optics in 1981. Horizontal and vertical bearings were later translated to x and y map coordinates. This transiting technique, developed by R. Payne, is described by Würsig (1978). The station was in use from 19 August to 1 September 1980, and 23 August to 13 September 1981.

Locations of most whales within a 10 km radius of the theodolite station during fair weather and daylight hours were documented. Unfortunately, whales rarely approached Herschel Island closer than 5 km during the 1980 field season, so details of behavior were difficult to discern. In 1981, fewer whales were seen, but they were closer to shore, allowing more detailed behavioral observations.

RESULTS

The Surfacing-Dive Cycle

In the Beaufort Sea in summer, nonmigrating bowhead whales typically alternate between dives of variable length, depending on activity, and surfacings within which there are several respirations. This pattern differs slightly from that during migration, when sounding dives (around 15 min long) are separated by periods when several brief surfacings, each with a single respiration, alternate with "series" dives about 15 s long (Rugh and Cubbage 1980; Carroll and Smithhisler 1980). Presumably, migrating animals dive between respirations to avoid hydrodynamic drag imposed by the air-water interface. No such submergence is necessary for a whale that is not moving rapidly through the water. However, the basic repertoire of breathing several times in relatively, closely spaced series and then not breathing for many minutes (during the long dive) is similar during both prolonged directed movement and more stationary activity. The pattern extends to some degree even to whales that remain at the surface for long periods (up to 30 min or more during surface skim feeding, socializing, or play). They generally breathe several times within a few minutes, and then cease breathing for a longer time, despite their near proximity to the surface and the availability of air. Similar patterns are seen in other whales, including right whales, *Eubalaena glacialis*, (Kraus et al. 1982) and gray whales, *Eschrichtius robustus*, (Sumich 1983). Durations of surfacings and dives, intervals between successive blows, and number of blows per surfacing are described in Würsig et al. (1984).

Surfacing and Respiring

Whales in water deeper than about 30-45 m usually surface head and blowhole first after a sounding dive, with the body oriented at some angle (such as 30°) from horizontal. When whales do not dive very deeply (as in shallow water), the surfacing is less due to active swimming upward, and the head and tail surface at approximately the same time.

A blow is an exhalation of air by a whale. Blows can occur above or below the surface. Surface blows are usually visible as a white cloud of water spray, but may be so weak as to be undetectable. The first blow after a surfacing usually appears strong, probably because it is a more forceful exhalation and because water is present above the blowholes during or just after surfacing. On calm days and when whales lie at the surface with the blowholes exposed, the blowholes are relatively dry, and blows may be difficult to detect. Blows of calves can also be difficult to see.

Surface exhalations of gray; humpback, *Megaptera novaeangliae*; fin, *Balaenoptera physalus*; and southern right whales, *Eubalaena australis*, are almost always followed immediately by an inhalation (B. Würsig, pers. obs.). Hence we suspect, following Scoresby (1820), that exhalations and inhalations generally occur together in bowhead whales as well.

Diving and Associated Behavior

The predive flex is a distinctive concave bending of the back seen several seconds before many dives. The whale flexes its back by about 0.5-1 m, so that the snout and tail disrupt the surface. Considerable white water is created at these two points. The whale then straightens its back and lies momentarily still before arching the back convexly as it begins its roll forward and down. The predive flex is seen from low vantage points as an abrupt lifting of the head, because the flukes apparently only touch the water surface from below.

The predive flex was seen more often during 1980 than during 1981 or 1982. Although it occurred previous to dives well over 50% of the time in 1980, it occurred in only 8% of the observations (before 29 of 352 dives) in 1981. For 1982, we have especially detailed analyses of predive flexes. In that year, predive flexes occurred in presumably undisturbed noncalves before 32 of 132 dives (24.2%); flexes occurred more often in late August than earlier (Table 1). Dives following predive flexes were, on the average, about twice as long as dives without predive flexes (19.00 $\pm$ SD 7.877 min, n = 13, vs. 10.15 $\pm$

TABLE 1.—Dives preceded by a predive flex among noncalf bowheads early and late August 1982. The frequency of occurrence is significantly higher after 19 August (chi-square = 4.29, df = 1, $0.025 < P < 0.05$).

	Up to 19 Aug. 1982	After 19 Aug. 1982	Total
Dives with predive flex	9	23	32
Dives without predive flex	49	51	100
Total	58	74	132

7.465 min, $n = 36$; Mann-Whitney U = 97.5, $P < 0.01$). Five dives were preceded by two predive flexes, with the flexes separated by a blow. Two dives were preceded by three flexes. We have no data on durations of dives following multiple flexes.

During the dive, which can at times be predicted by the predive flex, the whale makes its body convex and pitches forward and down. If the angle of submergence is steep, the tail is usually raised above the surface; if not, the tail may remain below or just touch the surface. Rarely do bowheads sink down without visibly arching the back.

In 1982, 59 of 138 dives (42.8%) were preceded by raised flukes. Of the 32 dives preceded by one or more predive flexes, 21 also showed raised flukes. These two predive behaviors tended to occur together ($\chi^2 = 3.94$, $P < 0.05$, df = 1), and dives with raised flukes were significantly longer than those not preceded by raised flukes (18.67 ± SD 9.966 min, $n = 12$, vs. 10.05 ± 6.956 min, $n = 38$; Mann-Whitney U = 114, $P < 0.01$).

There was no difference in durations of surfacings concluded with and without raised flukes. However, surfacings including predive flexes tended to be longer than those without predive flexes (3.09 ± SD 1.038 min, $n = 14$, vs. 1.79 ± 1.284 min, $n = 52$; $t = 3.50$, df = 64, $P < 0.001$), probably because durations of surfacings and dives are correlated (Würsig et al. 1984).

The function of the predive flex is unknown. Flexes occur more often before longer dives (which may take the whales deeper in the water column). Raising the flukes before a dive appears related to the steepness of the dive; whales that roll forward while dropping the front of the body at least 30° below the water surface usually raise their flukes. The weight of the raised tail stock in the air must help propel the animal downward (much as human skin divers raise their legs above the surface during the initiation of a steep dive). Although raised flukes are common during steep dives in many whales, the predive flex has not been reported in other species.

The Underwater Blow

The underwater blow is a burst of air emitted underwater. The bubble burst is circular and up to 15 m in diameter when it arrives at the surface. Release of air underwater was recorded about 10 times via nearby (< 1 km away) sonobuoys; the noise was detectable for 3-4 s, but the white water and expanding concentric wave were visible much longer. On one occasion, we definitely saw that the air came from the blowhole rather than the mouth, and we believe that this is always true. We saw underwater blows immediately after whales dove and just before they surfaced, but more usually in the middle of the dive, when the whales were out of sight.

Underwater blows were most frequent in 1980 during periods of pronounced feeding in water < 14 m deep (see Feeding section). In 1980, we saw 158 underwater blows in 30.4 observation hours; in 1981, 57 blows in 30.8 observations hours; and in 1982, only 6 blows in 36.5 observation hours. (The difference between years is statistically significant; $\chi^2 = 189$, df = 2, $P < 0.001$.) Concurrently, whales tended to be found in progressively deeper water from 1980 to 1982.

Underwater blowing occurred more often in the morning and evening than around solar midday in both 1980 and 1981 (Fig. 4; solar noon occurs about 1500 MDT in the eastern Beaufort Sea). The midday "lull" in underwater blowing coincided with a peak in frequency of socializing, the main nonfeeding behavior observed (see Social Behavior section below). Nemoto (1970) suggested that baleen whales in general show a high level of feeding activity in the

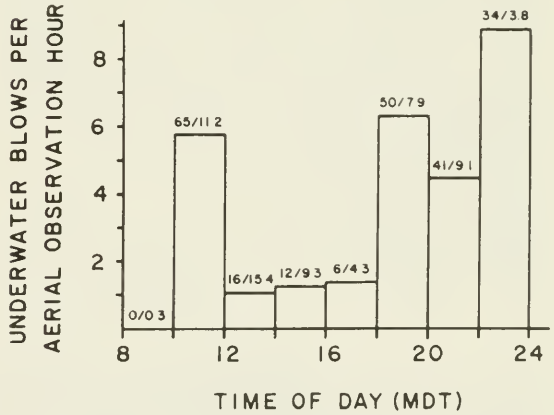

FIGURE 4.—Number of underwater bowhead whale blows per aerial observation hour in relation to time of day, 1980 and 1981 combined. There were few underwater blows in 1982. The numbers at the top of each column are number of blows seen/number of observation hours.

morning and a lower level during midday, but we have no direct evidence of this in bowheads.

Although underwater blows seem to occur more often in shallow water when whales may be feeding, we have not included this behavior as a definite part of feeding. There is only a general similarity to bursts of bubbles associated with feeding humpback whales in the North Atlantic (Hain et al. 1982), and the bubble nets reported for humpbacks by Jurasz and Jurasz (1979) are very different.

Social Behavior

Behavior was termed social when whales appeared to be pushing, nudging, or chasing each other, or when they were within half a body length of one another. Whales within half a body length almost always stayed close to each other, and oriented towards each other or interacted in some manner. Thus, our use of proximity as an indication of sociality was appropriate. Interactions between mothers and calves, and between whales skim feeding in close proximity, were not included as social interactions in this analysis. Whales may, of course, communicate by sound, and thus may socialize over far greater distances than those described here. Our sonobuoys often detected bowhead calls while socializing was underway. However, we could not verify whether acoustic communication was occurring between any particular whales, so we restricted our definition of socializing to visible behavior. Synchronous diving and surfacing over areas many kilometers in diameter (see below) may represent a different form of social interaction from what we discuss in this section. Because groups of whales usually could not be reidentified positively from one dive to the next, we treated observations of social behavior at intervals of > 5 min as independent for the purpose of counting number of interactions. Conversely, we did not score social behavior by one group more than once in 5 min when counting frequency.

Frequency of Socializing

Social behavior was seen less frequently in late August-early September than in early August, both in 1980 and 1981 (Table 2). Rugh and Cubbage (1980) and Carroll and Smithhisler (1980) reported a higher incidence of social interactions during the spring migration around Alaska than we saw at any time. The apparent waning of social activity from early to late August may be part of a continuing decrease from a higher level in spring.

Little socializing was observed in 1982. In presumably undisturbed whales, we observed only seven cases, all on 8, 19, and 23 August. Throughout August 1982, most whales were alone and making long dives. The overall socializing rate for each year (Table 2) demonstrates the dramatic decrease in socializing in 1982 compared with the two previous years. This decrease may be related to the increase in 1982 in the average distance from shore and depth of water at locations where bowheads were studied. However, we found no consistent trend for socializing to occur more often in shallow water than in deep water within 1 yr.

There was some indication of hour-to-hour variation in amount of social activity in all 3 yr (Fig. 5). In 1980 and 1981, it peaked around 1400-1600 MDT, the noon period by sun time. In 1982, the few (7) cases were recorded from 1600 to 2000 MDT, somewhat after solar noon (Fig. 5). In both 1980 and 1981, there was another peak after 2000 MDT. Why whales should engage in more social activity around noon (and possibly in the evening) than at other times is unknown. However, diel rhythms are well known in several mammals (e.g., Saayman et al. 1973 for bottlenose dolphins; Matsushita 1955 for sperm whales; Schevill and Backus 1960 for humpback whales). The increased level of socializing around noon may reflect a lowered level of feeding at that time, which Nemoto (1970) suggested for baleen whales in general.

Physical Interactions

During surface interactions with nearby whales, socializing whales often turned. In contrast, nonsocializing whales often surfaced and dove again without changing direction. In the 3 yr, turns oc-

TABLE 2.—Number of social interactions per aerial observation hour, divided into about 10-d periods, in 1980, 1981, and 1982. Only presumably undisturbed periods are included.

Year	1-10 Aug.	11-20 Aug.	21-31 Aug.	1-10 Sept.	Overall
1980	28/7.0 = 4.0	6/2.9 = 2.1	8/7.7 = 1.0	—	42/17.6 = 2.4
1981	14/4.3 = 3.3	12/5.5 = 2.2	9/3.3 = 2.7	4/4.0 = 1.0	39/17.1 = 2.3
1982	1/1.5 = 0.7	3/7.6 = 0.4	3/12.8 = 0.2	—	7/21.9 = 0.3

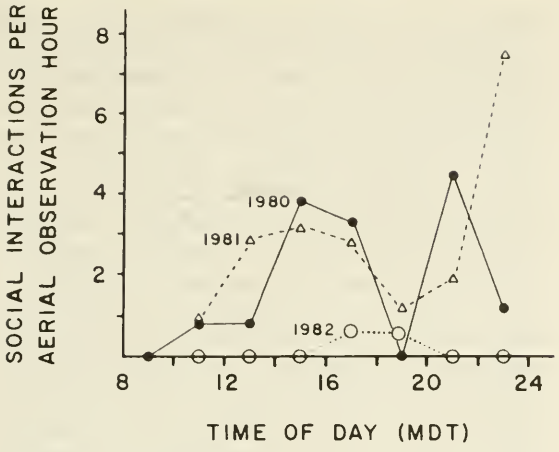

FIGURE 5.—Number of bowhead whale social interactions per aerial observation hour in relation to time of day.

curred during 53 of 133 (40%) surfacings with socializing, and in 128 of 484 (26%) without socializing ($\chi^2 = 9.04$; df = 1, $P < 0.005$).

When bowhead whales touched, they often appeared to push each other. Pushing or touching was usually done with the head, while oriented head to head, or head to tail. However, we also saw whales of adult size dive under the bellies of other whales and apparently nudge or push the other whales near their genital areas. At other times, whales dove under each other at very close range without any indication that they were touching.

Apparent chase sequences involved two or three whales in a line, usually < 2 body lengths apart. During these chases one whale often turned abruptly left or right, and the second (and third) followed. Movement was faster during chases than at all other times when we saw presumably undisturbed whales at the surface.

Both touching and chasing may at times represent low levels of sexual activity, but this is unproven because we cannot determine the sex of a bowhead whale from a distance. Payne and Dorsey (1983) and Tyack and Whitehead (1983) described physically interacting right and humpback whales, respectively, which appeared to be engaging in social-sexual activity.

Possible Mating

In 1981, we twice observed apparent mating. The more prolonged observation was on 10 August 1981, within a 25 km^2 area where there were 20-30 whales whose main activity was socializing. Two whales interacted for over 1 h with chases, flipper caresses, belly-to-belly orientation, rolls toward and away from each other, head nudges to the genital area and to the rest of the body, tail slaps, and flipper slaps. One whale, a recognizable animal that we termed "Whitespot", was about 1-2 m longer than the other ("B") and was the more aggressive. Although B originally nudged the genital area of Whitespot, it was Whitespot who appeared to initiate flipper caressing and rolls toward B. The two whales rolled their ventral surfaces together for about 5 s, but B then rolled its ventrum in the air in an apparent attempt to avoid ventral contact with the larger animal. As it rolled away from Whitespot, B defecated, and when Whitespot moved its head toward the genital area of B, B defecated two more times in rapid succession. B then dove away from Whitespot, and Whitespot followed it at the surface in an apparent chase. Whitespot then stopped and, alone at the surface, rolled two times and tail slapped while on its back. It then dove, and the two appeared together again at the surface 4 min later, with no further energetic surface interaction.

We do not know the sex of either animal, but it appeared that Whitespot was attempting to copulate with the reluctant animal. Some of us (Würsig and Payne) have observed southern right whale females frequently roll their ventra away from aggressive males, leaving their genital areas above the surface of the water, where the males cannot reach them. Everitt and Krogman (1979) photographed very similar behavior of a group of six bowheads off Barrow, AK, in May. Our observations here were highly reminiscent of such behavior. Although adult females are slightly larger than adult males in both right and bowhead whales, we commonly see large southern right whale males in pursuit of smaller females, which attempt to avoid the males.

On 25 August 1981, two bowheads briefly placed their ventral surfaces together and clasped each other with their flippers. After 1 min, they rolled apart, blew, and dove slowly as a third whale approached. The mutual rolling and leisurely diving indicated that, if this was copulatory behavior, it was mutually undertaken by the two whales in contrast to the previous example.

Group Structure and Stability

Two observations of recognizable bowheads provided evidence about group structure and stability. We observed a distinctively marked pair of adults, one accompanied by a calf, at about lat. 70°10′N, long. 133°50′W on 7 August 1980. We saw a similar-

ly marked group of two adults and a calf, almost certainly the same whales, on 20 August at lat. 70°07'N, long. 131°30'W, which is about 85 km from the place they had been seen 2 wk earlier. This observation suggests that some groups of bowheads are maintained for at least a few weeks. The observation also suggests that females with calves may sometimes be accompanied by escorts, as has been observed for wintering humpback whales (Herman and Antinoja 1977).

Feeding

Feeding appeared to occupy much of the time of the bowheads that we observed, but we had to rely on indirect clues, such as observations of swimming with open mouth, mud streaming from the mouth, or presence of feces in the water, to indicate that feeding had taken place. The four possible types of feeding behavior that we identified were 1) water-column feeding; 2) near-bottom feeding; 3) skim feeding; and 4) mud tracking. Of these, the first three rather clearly represented feeding, whereas the function of the last was less certain. As noted above, underwater blowing showed some association with feeding, but the connection was uncertain.

In 1980, certain feeding behaviors occurred in particular areas: only water-column feeding was seen near the Issungnak artificial island site (Fig. 1), whereas only skim-feeding was seen off the Tuktoyaktuk Peninsula near McKinley Bay. In 1981, there was less evidence for feeding, although we suspect that most feeding occurred in the water column. In 1982, when whales dove for long periods (up to 30 min), we suspected water-column feeding to be occurring at almost all times.

Water-Column Feeding

Water-column feeding could not be observed directly. Whales were scored as feeding in the water column when they dove for long periods, and when, between long dives, there was much defecation and only slow forward motion. Defecation is simply an indication of prior feeding. However, particular behaviors such as a series of long dives usually continued for many hours, so occurrence of defecations between long dives was considered indicative of ongoing feeding in the water column.

The frequency of apparent water-column feeding was not constant. In 1980, we saw bowheads water-column feeding from 3 to 22 August. Thereafter, few whales were present in the area where we had observed this behavior, and whales seen elsewhere did not seem to feed in the water column. In 1981, when we saw less defecation, we only scored as water-column feeding some adult whales that dove for prolonged periods on 24 August, while calves remained at the surface. In 1982, most whales made long dives. These whales probably were feeding in the water column, even though we saw little defecation at the surface. Feeding below the surface may have occurred during many other dives besides those that we classified as dives with water-column feeding.

Observations on 3 August 1980 typify water-column feeding behavior. On this date, bowheads were north of Kugmallit Bay where water depth was 18-38 m. The surface water was turbid, brackish water from the Mackenzie River, but beneath this surface layer, there was a second layer of clearer, saline Beaufort Sea water (Griffiths and Buchanan[7]). The whales occurred in groups of 2-10 animals, and occasionally as individuals without others nearby. Group members showed a high degree of synchrony, often surfacing very close together and remaining close at least until they dived again. Not only did the members of a group surface and dive synchronously, but various groups spread over an area several kilometers in diameter all tended to be at the surface or beneath it at the same time.

While the animals were at the surface, they moved slowly forward while taking a series of breaths. As each individual dived, it raised its tail clear of the water, and disappeared from view in the turbid water. Thus, these dives must have taken the whales well below the surface. When the whales were at the surface, they often disturbed the turbid surface layer, exposing dark patches of seawater from deeper depths. However, while submerged after a dive that was preceded by raised flukes, they did not affect the thin surface layer, indicating that they were probably feeding in the underlying clearer ocean water. Defecation was frequent, suggesting that feeding may have taken place recently. The feces clouds were red-orange.

Bottom Feeding

On 12 August 1980, we noticed clouds of mud suspended in the water about 25 km west of Issung-

[7]Griffiths, W. B., and R. A. Bachanan. 1982. Characteristics of bowhead feeding areas. *In* W. J. Richardson (editor), Behavior, disturbance responses and feeding of bowhead whales *Balaena mysticetus* in the Beaufort Sea, 1980-81, p. 347-455. Unpubl. Rep., 456 p. LGL Ecological Research Associates, Inc., Bryan, TX, for Bureau of Land Management, U.S. Department of the Interior, Washington, DC. Available from Minerals Management Service Alaska OCS Region, P.O. Box 101159, Anchorage, AK 99510.

nak artificial island (Fig. 1). The clouds represented suspended mud and not plankton because the material was of the same color as mud dredged up by industrial activities. Whales surfaced with large amounts of muddy water streaming from their mouths, indicating they had been feeding from or near the bottom. This behavior occurred in 24-29 m of water and seemed very localized. We saw no indication of bottom feeding in the same area on 22 August 1980, but we had observed similar mud clouds nearby on 9 August, when prolonged observations were not possible. On 25 August 1981, whales again surfaced with mud streaming from their mouths. The location was 15 km south of the position where we observed such behavior in 1980; water depth was only 10-13 m.

These are, to our knowledge, the first published behavioral observations of apparent near-bottom feeding by bowhead whales. However, Johnson et al. (1966), Durham (1972), and Lowry and Burns (1980) detected pebbles and bottom-dwelling species in bowhead stomachs.

Bottom-feeding whales were usually separated from other whales by 150-300 m when at the surface. On 12 August 1980, at least 10 whales were bottom feeding within an area of 3 km radius. Whether they were feeding on inbenthic or epibenthic invertebrates we do not know. In the eastern Beaufort Sea, the average biomass of inbenthic animals greatly exceeds that of epibenthic animals (Griffiths and Buchanan footnote 7). However, the latter may occur in dense swarms in certain places. For a balaenid whale, such swarms would seem to be a much more suitable type of food than inbenthic organisms. Mud might be taken inadvertently along with epibenthic animals.

Skim Feeding

The only feeding type that we observed directly was skim feeding. In the third week of August 1980, we observed whales moving slowly and deliberately at the surface with their mouths open wide. Usually the rostrum just broke the surface of the water, and was parallel to it. In these cases, the lower jaw was dropped to varying degrees, as could be seen from the depth of the white chin patch. In 1980, skim feeding was observed along the Tuktoyaktuk Peninsula in water 12-22 m deep. Whales occasionally skim fed alone, but more often did so in groups of 2-10 or more individuals. During any one observation period, they stayed in the same general area by repeatedly turning and did not appear to make any net geographic movement. However, we found groups of skim-feeding whales in different locations on different days.

During 1981, we witnessed skim feeding on a large scale only on the evening of 18 August, 32 km NNW of Pullen Island in water 25 m deep. About 20-30 whales in the 25 km^2 area were swimming with mouths open; they travelled slowly, usually just below the surface ($\sim$ 2-3 m deep). Copepods were unusually abundant in near-surface waters at this location and time (Griffiths and Buchanan footnote 7). On 23 and 24 August 1981, we saw one isolated example on each day of a whale feeding at the surface briefly (observed for < 1 min) in approximately the same area as on 18 August.

Typically, skim-feeding whales were oriented with their backs at the water's surface. However, they occasionally swam on their sides with mouths open at an angle of about 60°, and once we saw two whales separated by three body widths swimming on their sides, belly to back. In one instance, a skim-feeding whale swam inverted for at least 3 min, with the underside of its chin at the surface.

Frequently, the skim-feeding whales swam in echelon formation, each whale swimming just behind the preceding whale, but offset laterally by one-half to three body widths, reminiscent of geese in V formation (Fig. 6). At other times, they swam abreast and parallel to one another. Videotape from 18 August 1981 showed that whales within the echelons were a mean of 0.53 whale lengths apart (SD = 0.599, n = 66), or about 8 m. These distances were measured from different echelons or from the same echelon at intervals of at least 5 min. We videotaped a recognizable whale for almost 3 h on this day as it skim fed in changing echelon formations, usually taking the lead position. Echelons were clearly dynamic in terms of membership, size, and organization. In 1981, the mean echelon size was 4.7 animals (SD = 4.05, n = 23). While the largest such formation observed in 1980 contained 5 individuals, the largest in 1981 contained 14 animals.

We suspect that echelon feeding increases the feeding efficiency of those animals staggered behind and to the side of other individuals, perhaps by helping them to catch prey that escape or spill from the mouth of the whale in front, or by reducing the ability of prey to escape to the side. Skim feeding in echelon may allow more effective exploitation of concentrated patches of small prey than would be possible if whales were feeding alone. If so, the change in efficiency that accrues when echelons are formed may have an important cost/benefit effect on energy expended per whale. The predominant prey types of bowheads include copepods and euphausiids (Lowry

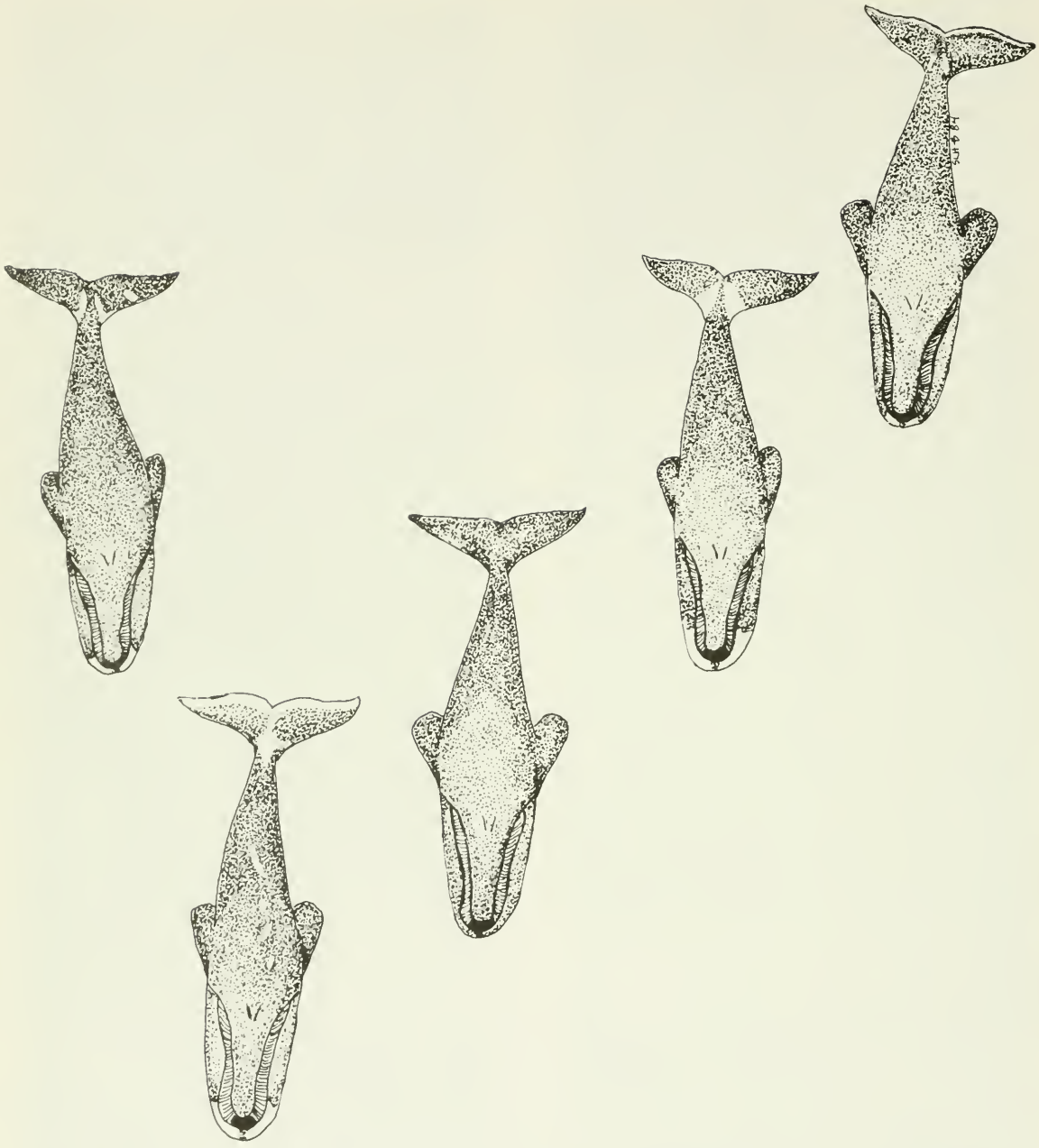

FIGURE 6.—Five bowhead whales skim feeding in echelon formation. Drawing after a 35 mm photograph and video footage from the air.

and Burns 1980). The latter are adept at avoiding most sampling gear because of their rapid movement. However, bowheads at times collect euphausiids in very large numbers, despite the bowhead's slow swimming speeds relative to the better known euphausiid predators such as rorquals. Perhaps echelon feeding is especially helpful in catching fast-swimming prey such as euphausiids.

During 1982, little direct evidence for feeding was noted. We saw no skim feeding at the surface, and noticed only nine isolated instances when a whale's mouth appeared to be open slightly. These brief, slight

openings of the mouth contrasted sharply with the sustained large gapes observed in 1980 and 1981, and probably did not represent feeding. In southern right whales, Payne (pers. obs.) has observed mouth opening that he interprets as yawning following sleep.

Mud Tracking

Mud tracking occurred when whales swimming in shallow water (< 12 m depth) disturbed the bottom sediments with each fluke beat, producing clouds of mud joined by a narrower trail of muddy water. These elongated clouds of mud were different from mud clouds produced during presumed bottom feeding. Although we often could not see the whales, in at least a few instances their mouths were open. We saw mud tracking during only three flights in the third week of August 1980.

Mud tracking probably represented incidental disturbance of bottom sediments by a whale feeding near the bottom in shallow water. We saw no evidence that bowheads ever turned and swam back along a mud track made previously. The mud tracks tended to be straight, and some extended for well over 1 km. At certain times, clouds of mud streamed from the whale's body as it swam near the surface. In this case, we suspect that the whales had contacted the bottom, and that the mud had stuck to their bodies. Sometimes, mud-tracking whales exhaled while submerged, producing a characteristic burst of bubbles (see section on The Underwater Blow).

Defecation

Defecation usually was evident as a cloud (2-3 m diameter) of red-orange feces near the surface. Whales almost invariably were moving forward or diving when they defecated, and over 50% of the bowheads observed defecating in 1980 did so while the tail was arched up high out of the water just before the dive. The anus was thus close to or at the surface. No part of the body appeared to touch the feces cloud, which was visible at the surface for up to 10 min. When whales moved forward while defecating, the feces were more dispersed and disappeared within 1-2 min. Brown (1868) noted that feces of eastern arctic bowheads were also red. Renaud and Davis[8] observed red clouds of feces off the Tuktoyaktuk Peninsula in 1980.

Defecation was seen more often in 1980 (23 cases during 30.4 h over whales) than in 1981 (11 cases during 30.8 h over whales). The difference is statistically significant ($\chi^2 = 4.39$, df = 1, $0.025 < P < 0.05$), and may be related to year-to-year differences in feeding patterns. In 1982, we saw only one defecation (by a lone whale playing with a log). Because we can only observe defecations by whales at the surface, we compared the rates in reference to the number of whale-hours of observation at the surface. In 1980, there were 2.29 defecations/whale-hour at the surface, as opposed to 0.73 in 1981, and 0.09 in 1982 ($\chi^2 = 27.58$, df = 2, $P < 0.001$). This decrease could result either from decreased defecation (indicative of less feeding), or from an increasing tendency to defecate under the surface where we could not observe it. During 1982, dives were longer than in the 2 previous years (Würsig et al. 1984), and we suspect that much water-column feeding was taking place.

Adult-Calf Pairs

Calves of the year are a light tan color, distinct from the dark black of noncalf bowheads. An adult that remained close to a calf was assumed to be the calf's mother. For the closely related southern right whale in winter, Payne and Dorsey (1983) found that in unambiguous adult-calf pairs, the adult was always a female, and that identified calves were always seen with the same individually identified female. At times, we saw apparent nursing as calves submerged briefly, oriented toward the teat region of the adult. In 1982, we made longer observations of calves than in either 1980 or 1981.

The relative lengths of six calves measured from videotape sequences recorded during August 1981 were a mean of 0.57 ± SD 0.052 adult body lengths. Many of the calves we observed in August 1982 appeared to be smaller, about one-third adult size. This is corroborated by the fact that 14 calves measured via photogrammetry in August-early September 1982 were 4.1-7.6 m long, or 33-45% (mean 41%) of the length of the accompanying adult (Davis et al.[9]). It may be that births occurred earlier in the year in 1981 than in 1982, or that the females videotaped in 1981 were smaller, on average, than those measured in 1982.

[8]Renaud, W. E., and R. A. Davis. 1981. Aerial surveys of bowhead whales and other marine mammals off the Tuktoyaktuk Peninsula, N.W.T., August-September 1980. Unpubl. Rep., 55 p. LGL Ltd., Toronto, for Dome Petroleum Ltd., Box 200, Calgary, Alberta T2P 2H8, Canada.

[9]Davis, R. A., W. R. Koski, and G. W. Miller. 1983. Preliminary assessment of the length-frequency distribution and gross annual reproductive rate of the western arctic bowhead whale as determined with low-level aerial photography, with comments on life history. Unpubl. Rep., 91 p. LGL Ltd., Toronto, for National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115.

When an adult and calf were both at the surface, they were usually within one adult-length of each other. Videotape sequences showed the mean distance apart to be 0.61 adult whale lengths (SD = 0.564, n = 8, range = 0.1-1.5), or about 9 m. The calves spent most of the time lying beside the adult, and facing in the same direction as the adult. At times, the calf strayed up to two whale lengths from the adult, and then oriented toward the adult. While the adult lay at the surface, the calf often submerged near the belly of the adult with its tail close to the adult's tail. This position is probably indicative of nursing. The calf then often swam under the adult, surfaced on the other side, respired one or two times, and submerged again toward the adult's belly, alternating sides with each surfacing. The calf also appeared at times to rest, lying quietly on the back and tail of the adult.

Calves were sighted at similar frequencies in all 3 yr (Table 3). However, durations of surfacings by calves were longer in 1982 than in 1980-81. Because of this, calves accounted for 15% of whale-hours of observation in 1982, but only 3% in 1981, and 4% in 1980 (Table 3).

Calves Alone

In 1982, calves spent almost 40% of their time at the surface unaccompanied by an adult. This was comparable with their behavior in 1981, but unlike 1980 when they were rarely seen alone. (Table 3).

On 24 August 1981, we saw three calves separated from each other and from the closest adults by 100 m to more than 300 m. It was, therefore, often not possible to assign calves to particular females. The nearest adults spent much time submerged, but the calves remained stationary at the surface. At one point, we videotaped an adult that surfaced 4.9 adult lengths from a calf lying stationary at the surface. During another videotaped sequence, an adult-calf pair, 0.2 lengths apart, was separated from a lone calf by 7.6 adult lengths. We suspect that the adults were feeding in the water column while calves waited at the surface.

In 1982, we observed four lone calves at the surface, on 18, 19, and 23 August, and on three of these occasions we saw the calf rejoin its presumed mother. On 18 August, a lone calf surfaced and oriented straight toward an adult at a distance of 1.6 km. When it came within 75 m of the adult, the adult also began to swim rapidly toward the calf. During a second incident on the same day, a calf and adult swam rapidly toward each other from at least 300 m distance. In both cases, the two dove simultaneously after coming together. On 23 August 1982, an adult surfaced 180 m from a lone calf, and the adult oriented toward the calf. When the two whales were $\sim$ 120 m apart, the calf also oriented toward the adult, but the adult was mainly responsible for closing the distance between them, as it swam at medium speed toward the calf. When the two whales were $\sim$ 20 m apart, the calf dove and reappeared 18 s later, reoriented by 180°, lying to the right of the adult, and facing in its direction. The calf then

TABLE 3.—Calf sightings and observation time in 1980, 1981, and 1982. Only flights with behavioral observations are considered, and both presumably undisturbed and potentially disturbed periods are included. The number of sightings of calves is an approximate count because multiple counts of the same calf were possible in cases where the calf and its mother were not individually recognizable.

	1980	1981	1982
No. sightings of calves	12	16	16
No. flights	14	18	14
Calf sightings/flight	0.86	0.89	1.14
Hours in plane over whales	30.4 h	30.8 h	36.5 h
Calf sightings/hour	0.39	0.52	0.44
Calf time at surface with mother	20.4 min	17.5 min	63.1 min
Calf time at surface alone	1.6 min	12.7 min	38.2 min
Total calf time at surface	22.0 min	30.2 min	101.3 min
% of calf surface time alone	7.3%	42.1%	37.7%
Whale-hours of observation at surface	10.03 h	14.98 h	10.95 h
Calf-hours of observation/ whale-hour of observation	0.037	0.034	0.154
Calf time at surface/ sighting	1.57 min	1.89 min	6.33 min

submerged several more times toward the belly of the adult, probably nursing.

Our observations of adults and calves orienting accurately toward one another at distances up to 1.6 km apart suggest that there was acoustic communication between the two. There is possible evidence for this from the incident on 23 August 1982. The rate of low-frequency tonal frequency-modulated calls, which we suspect to be long-distance contact calls, increased while the mother and calf were swimming toward each other from some distance apart, and then ceased altogether once the two whales were joined. Several unusual higher pitched calls of undetermined origin were also recorded by a sonobuoy near the calf while the two whales were separated.

Nursing

When the lone calf of 23 August 1982 joined its mother after a separation of at least 71 min, we observed the longest probable nursing bout seen during the study. As the two animals approached each other head on, the calf dove out of sight for the first apparent nursing dive when they were still about 22 m apart. The calf dove toward the teat region of the adult six times in all, with submergences lasting 18, 11, 27, 17, 12, and 10 s (mean = 15.8 ± SD 6.37 s). These brief dives were separated by brief surfacings lasting 6, 6, 9, 11, 23, and 17 s (mean = 12.0 ± SD 6.75 s). Each surfacing included a single respiration. Nursing ended as the calf and adult dove out of sight at the same time. Although there was no apparent progression in the durations of the calf's nursing dives over the entire nursing bout, surfacings tended to lengthen, suggesting an appeasement of the calf's eagerness to nurse. The duration of the probable nursing bout from the start of the first nursing dive to the start of the deep dive by both mother and calf was 2.78 min.

The other bouts of probable nursing were shorter, sometimes < 1 min, and involved adult-calf pairs that had not recently been separated, as far as we knew. Usually, all that we could see was one or two short dives by the calf toward the teat region of the mother at the end of a surfacing sequence, followed immediately by a dive by both animals.

Other Behaviors

Aerial Activity

Bowhead whales sometimes leaped or breached from the water, forward lunged, or slapped the tail or a pectoral flipper onto the water. During breaches, 50-60% of the body length left the water. The whale emerged head first at a small angle from the vertical, usually with the ventrum down. It then twisted and fell back onto the water on its side or back. Forward lunges differed from breaches in that the body came out of the water at a shallower angle and did not twist; the whale reentered belly first. The forward lunge had a larger forward component than did the breach.

Breaches, tail slaps, and flipper slaps sometimes occurred in bouts. Within bouts, intervals between successive breaches were generally greater than those between tail or flipper slaps. For example, breaches, tail slaps, and flipper slaps by one whale that engaged in all three behaviors on 6 August 1980 were at average intervals of 46, 8, and 4 s, respectively.

The incidence of aerial activity was comparable in the 3 yr (0.60, 0.93, and 0.82 bouts/whale-hour in 1980, 1981, and 1982), but much lower than reported for spring migration. Rugh and Cubbage (1980) saw breaching by 23% of all bowheads (n = 280) observed passing Cape Lisburne, AK, in spring.

Play

Although many social interactions may involve play, we could not distinguish low levels of mating activity or aggression from play. We scored play behavior only when whales spent some time at the surface associating with an object other than a conspecific. We saw no such behavior in 1980, but several incidents in 1981 and 1982. Few such interactions have been described for other baleen whales.

LOG PLAY.—We witnessed whales playing with logs in the water on two occasions in 1981, and once in 1982. Log play, which consisted of a whale nudging, pushing, or lifting a log, lasted 5 s, 10 min, and at least 1.5 h during these three observations. In 1981, other researchers saw bowheads playing with logs twice in the same general area as our 1981 observations (C. R. Evans and J. Hickie[10]). During two of our three observations the water was ensonified by noise pulses from distant seismic exploration (Richardson et al. in press). However, there was no proof of a connection between log play and seismic noise.

Some elements of log play by bowheads were similar to play with seaweed observed in southern

[10]C. R. Evans, Biologist, and J. Hickie, Biologist, LGL Ltd., Environmental Research Associates, 22 Fisher St., King City, Ontario L0G 1K0, Canada, pers. commun. September 1981.

right whales (Payne 1972). Both involved lifting the object with the head, moving the object along the back, and patting it with the flippers. Two log-playing bowheads attempted to push the log under water with the head. This action was reminiscent of a motion commonly made by male right whales when attempting to mate with uncooperative females (Payne, pers. obs.).

CALF PLAY.—On two occasions in 1982, lone calves at the surface interacted with debris in the water, and the actions had the appearance of play.

The first incident occurred over 12.3 min on 19 August 1982, when a lone young-of-the-year calf followed a line of surface debris ~ 2 m wide, probably composed mainly of invertebrates. The calf stayed at or just below the surface and oriented directly along the windrow, changing course as the line meandered left or right. Although the calf appeared to have its mouth open slightly for brief periods, it did not appear to feed extensively, if at all. However, its movements thoroughly disrupted and dispersed the line of debris. The movements were rapid and jerky, reminiscent of any uncoordinated young mammal. The calf lunged forward while in the debris on three occasions, and slapped its tail onto the water surface twice. For ~ 30 s, it moved rapidly along the line, ventrum up, with rapid up-and-down movements of the tail for the entire time. The sequence ended when the calf dove out of sight at the end of the windrow; we did not see it with an adult. Although the incident did not seem to represent concerted feeding, this "play" by the calf may have been practice in skills required for feeding.

A second incident of "calf play" occurred on 23 August 1982. This calf was first encountered hanging quietly just below the surface, or moving forward very slowly. During slow movement, it entered an area marked by dispersed fluorescein dye from one of our dye markers (see section on Methods). The dye covered an area about 40 m by 100 m. Immediately upon entering the area of bright green water, the calf became active. During the 22.3 min of association with the dye, the calf rolled ventrum up eight times for 5-20 s each time, and moved back and forth within, and to the edge of, the dye-clear water interface. Although not as active and not beating its tail as fast as the calf in the windrow, this calf made abrupt turns of $> 90°$ on 25 occasions during its stay in the dye, reorienting itself at the dye's edge in order to remain within the dye. The calf ultimately moved out of the dye and oriented toward an approaching adult. When the two joined, the calf apparently began nursing.

Synchrony of Activity and Orientations

There was often an impressive degree of synchrony of basic behaviors among members of quite widely spaced groups. We observed apparent synchronization of behaviors on time scales ranging from seconds to days.

Synchrony in General Activity

During 1980, we found that all or most bowheads in various areas did the same thing for up to several days. Some days later, the whales had usually moved, and whales were then found elsewhere engaged in different activities. For example, on 3 and 5 August 1980, whales north and east of Issungnak artificial island were mainly engaged in water-column feeding, with frequent defecation. By 6 and 7 August, whales in this area shifted to more surface-active behavior, interacting in groups with pushes and apparent chases. We saw little defecation at this time. On 12 August, at least 15 animals about 30-40 km west of this area were all apparently bottom feeding.

Whales were encountered in two additional areas in 1980: east of Pullen Island (19 and 20 August) and just west of McKinley Bay (19-22 August). In the Pullen Island area, all whales were mud tracking as described above. In the second area, mud also was evident, but there was much less underwater blowing. Some animals had mouths open at the surface. On 22 and 23 August 1980 almost all whales we encountered were skim feeding in groups of 10-30 animals north of McKinley Bay. However, in the Issungnak area farther west, substantial numbers of whales were still water-column feeding. On 27, 29, and 31 August 1980, whales interacted in small groups of 2-5 individuals. Some small groups oriented SSW, perhaps indicating the beginning of migration.

In summary, during 1980 (but not 1981 or 1982) we found that whales in various areas did much the same thing for up to ~ 5 d, but then shifted location, activity, or both. A partial explanation for the synchrony of behavior seen in 1980 may be that whales moved to exploit new food resources, and that the most appropriate feeding mode changed according to site-specific conditions. In the subsequent 2 yr, it appeared that whales were doing more water-column feeding in deeper water, perhaps because of a more consistent food supply.

Synchrony in Dives and Surfacings

We sometimes had the impression that all whales

in an area were synchronizing their surfacings and dives. Many were too far apart to be in visual contact. Ljungblad et al (1980) also reported synchrony among whales engaged in water-column feeding ~75 km east of Kaktovik, AK. They reported that "... whales were observed on the surface almost at regular intervals and gave the impression of resting between dives; then, suddenly, no whales would be seen in any quadrant for several minutes."

Although synchrony in surfacings by animals far apart suggests acoustic contact between animals, it is not proof of communication over that distance. The synchrony could be established through independent responses to common external cues. It could also occur if the animals were close together and visually synchronized before observations began; the observed synchrony would then be a residual phenomenon that persisted because of whales diving and surfacing for similar lengths of time. None of these possible explanations – acoustic communication, common external cues, or residual phenomenon – can be either proven or discounted at this time.

Synchrony in Orientations

Analysis of orientations provides additional evidence that widely separated whales at times synchronize their behavior during summer. Our best data were from three flights in 1980 when we flew in a straight line. At these times, we counted each individual only once. Rayleigh and χ^2 tests (Batschelet 1972) show that whale orientations were significantly nonrandom (Table 4).

For flights when we circled to make detailed behavioral observations, we analyzed orientations using the first heading noted for each surfacing of a whale. Because we were making repeated observations on the same animal in some cases, any consistency in orientations during those flights is attributable in part to different whales, and in part to subsequent surfacings of the same whale. In 1980 and 1981, the whales were oriented nonrandomly during 7 of the 11 flights with enough data for analysis (Table 4). The headings changed from day to day, however, and bore no apparent relationship to the general behavior of the whales. In 1982, no significant departures from uniformity were found during any of the five flights with sufficient data for analysis.

The headings on the latest day with observations in 1980 and 1981 usually were not in the direction to be expected at the beginning of the westward migration. On 31 August 1980, most bowheads observed while we circled north of the Tuktoyaktuk Peninsula were oriented north, east, or south (mean 121°T (true), Table 4). However, later that day on a direct flight, we found other bowheads to be oriented toward the south (mean 189°T). In this same general area, Renaud and Davis (footnote 9) also recorded a slight eastward tendency for bowheads seen on 21-24 August 1980, but a significant southwestward tendency (236°T) on 3-4 September 1980. On 8 September 1981, most whales west of Herschel Island were oriented toward the northeast (62°T), again not the direction to be expected at the beginning of westward migration. These results support our impression that most of the whales we observed were not migrating.

TABLE 4.—Bowhead orientations, judged relative to true north from the air, 1980-81. Only during the direct flights was each observation known to represent different animals. During the circling flights, each whale was scored an unknown number of times (but only once per surfacing).

	No. of animals with these orientations									Vector mean	Rayleigh	Chi-square test
Date	N	NE	E	SE	S	SW	W	NW	Total	direction	test	*P*
Direct flights												
11 Aug. 1980	16	1	3	0	5	2	10	6	43	321°	<0.001	<0.001
12 Aug. 1980	7	5	16	5	7	6	9	2	57	bimodal	n.s.	<0.025
31 Aug. 1980	1	1	1	3	8	8	0	1	23	189°	<0.001	[1]
Circling flights												
31 Aug. 1980	4	4	6	3	11	1	0	2	31	121°	<0.05	/
10 Aug. 1981	0	3	0	2	0	4	0	1	10	—	n.s.	/
10 Aug. 1981	3	1	7	2	1	6	0	1	21	bimodal	n.s.	/
13 Aug. 1981	12	9	11	1	1	0	1	1	36	43°	<<0.001	/
18 Aug. 1981	2	5	10	5	6	1	2	1	32	111°	<0.001	/
18 Aug. 1981	3	0	0	0	0	1	6	0	10	289°	<0.005	/
23 Aug. 1981	0	4	1	1	0	0	0	0	6	62°	<0.02	/
24 Aug. 1981	1	0	3	2	5	8	10	5	34	243°	<0.001	/
6 Sept. 1981	1	7	2	1	0	2	3	3	19	—	n.s.	/
7 Sept. 1981	2	5	1	1	0	2	2	3	16	—	n.s.	/
8 Sept. 1981	1	8	3	1	1	0	0	0	14	62°	<0.001	/

[1] / means cell sizes too small for a chi-square test.

We do not know whether consistent orientations represented a type of social synchrony, or whether the whales independently reacted to environmental stimuli (such as currents or wave orientations). Norris et al. (1983) and Braham et al. (1984) reported gray and bowhead whales, respectively, that may have been feeding by stationing themselves against a current. Shane (1980) has reported a similar stationing against the current for bottlenose dolphins in Texas. Gray whales in lagoons have been observed to move in the same direction as the tidal current (Norris et al. 1977), but in that case movement may have been related to avoiding shallow water as the tide receded.

Miscellaneous Observations

Speed of Travel

In 1980 and 1981, some data were gathered on bowheads visible from Herschel Island. The whales were usually > 3 km from shore, and detailed behavioral observations were infrequent. However, speed was sometimes measurable with a surveyor's theodolite. Whales rarely changed direction within any one 30 s period, so we calculated speeds from theodolite readings taken within 30 s of each other. This criterion was changed to 60 s for 30 August 1981, when a whale was followed at the surface for a long period, and changed direction relatively little.

For 1980, average speed was 5.1 km/h (n = 18, SD = 2.93) at the surface, and 4.3 km/h (n = 4, SD = 0.79) below the surface. The 1980 speeds are comparable with the most reliable estimates derived by Braham et al. (1979) and Rugh and Cubbage (1980) for migrating bowheads: 4.8-5.9 km/h and 4.7 ± SD 0.6 km/h, respectively. However, based on additional data, Braham et al. (1980) estimated the mean speed at Point Barrow in spring to be 3.1 ± SD 2.7 km/h. Speeds during active migration along the coast of Baffin Island in fall were 5.0 ± SD 1.3 km/h (n = 22) based on theodolite observations from a cliff (Koski and Davis[11]).

On 30 August 1981, an adult whale traveling east was observed continuously for 1.52 h. Its behavior was unusual – it did not submerge during the entire time. Its mean speed was 2.3 ± SD 1.26 km/h, considerably slower than the speeds mentioned above. Its mean blow interval was 10.0 ± SD 13.55 s (n = 420), significantly lower than the mean for all other undisturbed whales observed from Herschel Island (14.6 ± 9.56; n = 60; t = 2.54, $P < 0.02$).

On 8 September 1981, a mother-calf pair was observed by theodolite for 1.8 h. The average speed of the calf was 8.9 ± SD 5.57 km/h (n = 28). During this rapid movement, the calf exhibited breaches, forward lunges, tail slaps, and flipper slaps.

Associations of Bowheads with Other Species

We saw several marine mammal species in the same general areas in which we observed bowheads: ringed seals, *Phoca hispida*; white whales, *Delphinapterus leucas*; and a gray whale. There was no obvious interaction between these species and bowhead whales. The gray whale was about 500 m from the closest bowhead. The Canadian Beaufort Sea is the extreme northeastern limit of the gray whale's summer range (Rugh and Fraker 1981).

Flocks of up to 50 phalaropes (*Phalaropus* sp.) were often present near skim-feeding bowheads. These birds often alighted on water that had been disturbed by the whales, sometimes only a few meters from the whales. Phalaropes and bowheads probably feed on some of the same plankton species. The whalers used the presence of phalaropes as an indicator of where "whale feed" was present and, therefore, where whales were likely to be found (J. R. Bockstoce in press). Aside from phalaropes, we noticed glaucous gulls, *Larus hyperboreus*; arctic terns, *Sterna paradisaea*; and unidentified gulls circling briefly over whales on eight occasions.

DISCUSSION

Activities of Bowheads in Summer and Other Seasons

From 1980 through 1982 we observed a steady progression in the August distribution of bowhead whales near Tuktoyaktuk from shallow water nearshore to deeper water farther from shore (Fig. 3; Richardson et al.[12]). Such a dramatic difference in distribution over the 3 yr may be due to many different ecological and behavioral factors. Disturbance

[11]Koski, W. R., and R. A. Davis. 1980. Studies of the late summer distribution and fall migration of marine mammals in NW Baffin Bay and E Lancaster Sound, 1979. Unpubl. Rep., 214 p. LGL Ltd., Toronto, for Petro-Canada Explorations, Calgary. Available from Pallister Resource Management Ltd., 700 - 6th Avenue S.W., Calgary, Alberta T2P 0T6, Canada.

[12]Richardson, W. J., R. A. Davis, C. R. Evans, and P. Norton. 1983. Distribution of bowheads and industrial activity, 1980-82. *In* W. J. Richardson (editor), Behavior, disturbance responses and distribution of bowhead whales *Balaena mysticetus* in the eastern Beaufort Sea, 1982. Unpubl. Rep., p. 269-357. LGL Ecological Research Associates, Inc., Bryan, TX, for U.S. Minerals Management Service, Reston, VA. Available from Minerals Management Service Alaska OCS Region, P.O. Box 101159, Anchorage, AK 99510.

by industrial activity in nearshore waters is also a possibility (see footnote 12). The fact that predominant feeding modes shifted from year to year is consistent with the "variable food supply" explanation. In 1980, whales in shallow water exhibited bottom feeding and skim feeding, while whales in slightly deeper water apparently fed in the water column. In 1981, most feeding appeared to be water-column feeding and skim feeding. In 1982, whales made long dives and presumably were often feeding in the water column.

Bowhead whales have finely fringed baleen, the longest of any whale species, and are adapted to strain small zooplankters from the sea. Stomach contents indicate that, at least in Alaskan waters, bowheads feed mainly on copepods, euphausiids, and amphipods (Marquette et al. 1982). Summering bowheads tend to occur at locations where copepod abundance is above average (Griffiths and Buchanan footnote 7). Lowry and Burns (1980) examined five whales killed off Barter Island, AK, in autumn and found about 60% copepods and about 37% euphausiids in their stomachs. However, all five whales may have fed at least partially near the sea floor; about 3% of the stomach contents consisted of mysids, amphipods, other invertebrates, and fish. Durham (1972) also suggested, based on stomach content analyses showing mud-dwelling tunicates, vegetation, silt, and small pebbles, that bowheads feed at times near the bottom. Lowry and Burns concluded from stomach content analyses that "...a feeding dive probably involves swimming obliquely from surface to bottom and back, feeding the entire time." Although this may be true at times, there is no direct information on underwater feeding behavior. We suspect that bowheads can detect concentrations of prey and open their mouths when appropriate. The bowhead whale is perhaps a more catholic feeder than once thought, capable of taking advantage of many different types of prey items at various positions in the water column and near the bottom. Year-to-year changes in distributions and availability of prey may account for the distributional changes that we have observed, but data on yearly changes in prey are lacking.

During spring migration around Alaska, bowhead whales appear to do little feeding; their stomachs usually are nearly empty (Marquette et al. 1982). On the other hand, feeding continues in autumn after bowheads have moved from the Canadian to the eastern part of the Alaskan Beaufort Sea (Lowry and Burns 1980; Marquette et al. 1982). Some feeding occurs in autumn as far west as the Point Barrow area (Lowry et al. 1978; Braham et al. 1984), and perhaps farther west off the Soviet coast (Johnson et al. 1981).

Feeding is not the only activity of bowheads in summer. Socializing, perhaps with occasional sexual activity, is also important. In 1982, however, there was less socializing than in 1980-81. Whales were in close proximity to each other less in 1982. This year-to-year difference in proximity may be related to the difference in type of feeding. While skim feeding at the surface, whales are often in close echelons. The proximity necessary for echelon feeding offers more chance for socializing, and socializing before or after feeding in echelon may be important to that mode of feeding. When whales appear to feed in the water column, however, they usually do not stay as close together. Thus, this type of feeding may neither require nor stimulate aggregations of animals, and the suspected predominance of water-column feeding in 1982 may explain the low socializing rate that year. Even when there is no close socializing, however, animals are often in a dispersed group within which acoustic communication is probably possible. Our observations of surfacing and dive synchrony by whales spread over distances of several kilometers indicate that they may have been in touch by acoustic communication.

The primary mating period of bowhead whales occurs in spring, including the spring migration (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Johnson et al. 1981; Nerini et al. 1984). We saw some evidence for sexual activity in the Canadian Beaufort Sea in both 1980 and 1981, but not in 1982. Even the active rolling at the surface that we observed in 1981, however, was not as boisterous as observed by Everitt and Krogman in spring. Also, we found an indication of less social activity in late August-early September than in early August. This apparent waning in social activity may be a continuation of the waning of sexual activity that started in late spring.

Many calves are born in winter or spring before the whales reach Point Barrow, although some may be born in early summer (Davis et al. footnote 9). During summer, the activities of female bowheads with accompaning calves are closely coordinated with those of their calves, and differ in some details from the activities of other adult bowheads (this study; Würsig et al. 1984). At least some calves remain with their mothers for the fall migration (Davis and Koski 1980). We know of no information concerning the age of weaning of bowhead calves, but in the closely related right whale, at least some calves remain with their mothers for 1 yr and ultimately separate from their mothers after returning to the

wintering area (Taber and Thomas 1982).

Aerial activity similar to what we observed in the eastern Beaufort Sea—breaches, tail slaps, pectoral flipper slaps, and rolls—has been observed in bowheads during spring migration (Rugh and Cubbage 1980; Carroll and Smithhisler 1980). It appears that aerial behavior is more frequent during spring migration than on the summer feeding grounds, and this may be related to the high levels of social-sexual activities during spring.

Comparisons with Other Baleen Whales

Bowhead whales spend their entire lives in arctic and near-arctic waters. This habit separates them from all other baleen whales, which may move into temperate or subtropical waters (Lockyer and Brown 1981). However, behavior is in large part determined by feeding mode and related ecological factors (Gould 1982), and here similarities between bowhead whales and several other species are evident.

Gray, bowhead, and right whales are often found in shallow water, and all three species feed on small invertebrates. Gray whales usually feed near the bottom (Bogoslovskaya et al. 1981; Nerini and Oliver 1983), whereas right and bowhead whales may skim their food at or near the surface (see Watkins and Schevill 1976, 1979 for right whales). But all three species are adaptable in feeding behavior. Gray whales apparently will feed on mysids associated with kelp (Darling 1977) or on crab *Pleuroncodes* in the water column (Norris et al. 1983). Right whales also feed below the surface, probably straining swarms of copepods and other small invertebrates in the water column (Pivorunas 1979). While it has long been known that bowhead whales feed at the surface and in the water column (Scoresby 1820), it was recently established from stomach content analyses (Durham 1972; Lowry and Burns 1980), and by observing bowhead whales surfacing with muddy water streaming from their mouths (this study), that bowheads sometimes feed near or on the bottom. It is not surprising that there are many similarities in the behavior of these species. Bowhead and right whales, in particular, are morphologically and taxonomically quite similar, and appear to obtain their food in very much the same ways. In fact, Rice (1977), mainly relying on a detailed comparison of morphology of bowhead and right whales, suggested that they be put in the same genus, *Balaena*.

The sleeker rorquals (Balaenopterid whales) generally gather their food more actively by lunging through concentrations of prey, and at least in the case of humpback whales, have developed complicated behavioral strategies for confining and concentrating their prey (Jurasz and Jurasz 1979; Hain et al. 1982). The rorquals are more often found in deeper water far from shore, and their behavior in general appears to be less similar to that of the bowhead whale than its behavior is to that of gray and right whales.

Gray whales spend part of the winter in warm water, near the shores of Baja California, and most of the summer they feed in the northern Bering and southern Chukchi Seas. Western Arctic bowheads make much shorter migrations, spending their winter in the pack ice of the Bering Sea and their summer predominantly in the Beaufort Sea. The two species thus use the Bering Sea at different seasons and for different purposes—gray whales to feed in summer and bowheads apparently to mate and calve in winter. Like bowhead whales summering in the Beaufort Sea, the primary activity of gray whales summering in the Bering and Chukchi Seas is feeding. However, both bowheads and gray whales (Sauer 1963; Fay 1963) occasionally socialize during summer.

Right whales, like bowhead whales, often appear to feed in the water column or at the surface (Watkins and Schevill 1976, 1979) and may stay in the same general area for days. While skim feeding, both species at times aggregate into echelons. In right whales, these echelons usually consist of only 3-6 whales (Payne, pers. obs.), while up to 14 bowhead whales have been seen skim feeding in echelon. However, Payne observed right whales during winter when little feeding occurs, so apparent differences in feeding details may be due to seasonal factors.

Apparent differences between the social activity of bowheads and right whales may also be largely attributable to the different times of year when they have been studied. The same kinds of nudges and pushes have been observed for interacting whales of both species, but the winter-spring social activity of right whales is much more boisterous than the summer social activity of bowheads. Observations of bowhead whales in spring indicate that their social-sexual activity at that season can be as boisterous as is seen in mating groups of right whales (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Rugh and Cubbage 1980; Johnson et al. 1981). The belly-up position of a female bowhead photographed in spring in the Alaskan Beaufort Sea (Everitt and Krogman 1979) indicates that females may attempt to evade potential mates who pursue them in large mating aggregations in the same way that female right

whales evade males in Argentine waters (Payne and Dorsey 1983). A photograph showing a remarkably similar mating group of right whales is shown in the article by Payne (1976). The fact that similar-looking social aggregations are seen in both species argues for a similar social system, although it does not show that the social systems are similar in all details.

Female right whales have young only at intervals of 3 yr or more (Payne, pers. obs.). The same appears to be true of bowheads (Davis et al. footnote 9; Nerini et al. 1984). This long calving interval may help to explain why bowhead and right whales have not made as dramatic a recovery from commercial exploitation as has, for example, the gray whale. Payne also found that right whale females that calve along the shore of southern Argentina in winter are usually not present in the years between calving. Each winter, a different segment of the population of mature females is present, in a 3-yr cycle. It is not known whether this cycling extends to the summer feeding grounds of these right whales. During the present 3-yr study, year-to-year variation in feeding and social behavior was dramatic, but we do not know whether this was due in part to some cyclic and synchronized activity of individual whales. We suspect that variable prey distibution was largely responsible.

ACKNOWLEDGMENTS

This project, including preparation of this paper, was funded by contracts from the Bureau of Land Management and the Minerals Management Service, U.S. Department of the Interior, to LGL Ecological Research Associates. We thank the Polar Continental Shelf Project of the Department of Energy, Mines, and Resources (Canada) for logistical help. Dome Petroleum Ltd. and Esso Resources Canada Ltd. shared data and assisted with logistics. NORCOR Engineering and Research Ltd. provided the Islander aircraft, and J. Merilees was its capable pilot. Personnel of the Beaufort Weather Office were helpful. K. Finley, P. Tyack, and R. Wells helped with aerial observations. K. Hazard, G. Silber, S. Taber, P. Thomas, and M. Würsig collected data from Herschel Island. C. Greene of Polar Research Laboratory set up the sonobuoy system. S. Heimlich-Boran prepared the illustrations of bowheads in this paper. J. Bird, L. Guinee, and V. Rowntree of the New York Zological Society, and C. R. Evans, R. Wells, and M. Würsig assisted with data analysis. H. Braham provided helpful suggestions on an earlier draft. We thank all of these organizations and individuals.

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FOOD HABITS OF BAIT-CAUGHT SKIPJACK TUNA, *KATSUWONUS PELAMIS*, FROM THE SOUTHWESTERN ATLANTIC OCEAN

LISA ANKENBRANDT[1]

ABSTRACT

Stomach contents of skipjack tuna captured in 1981-82 by live pole-and-line vessels off the southern coast of Brazil were analyzed for the presence of larval and juvenile skipjack tuna. The percentage frequency of occurrence, percent number, and percent volume were evaluated. Of the 1,041 stomachs that were examined for food, 436 were empty. The mean volume of food in all stomachs analyzed was 36.9 mL, of which 18.9 mL was bait and 18.0 mL was prey.

The gonostomatid *Maurolicus muelleri* and the euphausiid *Euphausia similis* were the principal foods. Other important foods were the chub mackerel, *Scomber japonicus*; the frigate tuna, *Auxis thazard*; gempylids; trichiurids; and carangids. In the study area, adult skipjack tuna were not found to feed on their young.

Kruskall-Wallis nonparametric one-way analysis of variance was used to test for differences in the mean volumetric ratios of food items in relation to skipjack size. The percentage of *E. similis* in the diet was found to decrease, while the proportion of *M. muelleri* was found to increase with increasing skipjack size. Seasonal variations in the diet were also examined and discussed.

Apparently the anatomy of their gill raker apparatus allows skipjack to ingest a wide variety of prey types above a minimum size. These variations in the food can be attributed to the number and size of the prey species in an area.

A Brazilian skipjack pole-and-line fishery has been developing in the Rio de Janeiro area since 1979 (Fig. 1). Because skipjack tuna, *Katsuwonus pelamis*, is one of the major tuna species harvested at maximum sustainable yield in the tropical and subtropical oceans (Kearny 1976; Evans et al. 1981), estimation of the fishery potential requires information on the distribution and concentration of its spawning stock. One technique used to determine the existence of a spawning stock is to quantify the distribution of its larvae. Obviously, the presence of large numbers of larvae would indicate a spawning stock occupies an area.

Knowledge of the distribution and abundance of juvenile skipjack tuna is limited. Occasionally, specimens have been found in experimental plankton hauls or in the stomachs of apex predators (Kearny 1976). From ichthyoplankton surveys, Matsuura (1982) and Nishikawa et al. (1978) reported larvae in warm tropical waters north of the study area (Fig. 1), and juvenile skipjack tuna have been found in the stomachs of adult skipjack tuna captured off west Africa and in the Caribbean (Suarez-Caabro and Duarte-Bello 1961; Klawe 1961; Dragovich 1970; Dragovich and Potthoff 1972). Their occurrence in the diet of central and south Pacific skipjack tuna caught by pole-and-line has been used to deduce their distribution and abundance (Waldron and King 1963; Nakamura 1965; Argue et al. 1983).

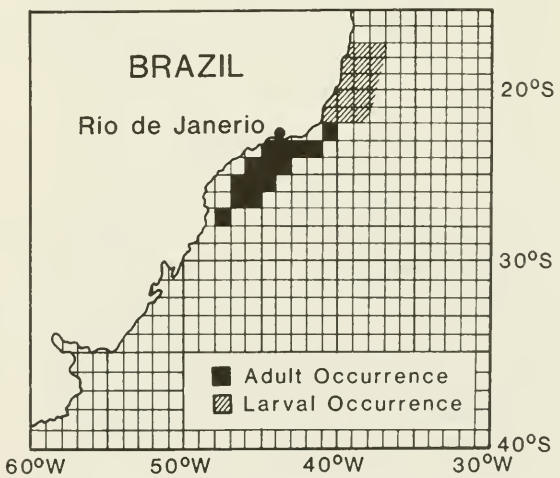


FIGURE 1.—Solid area indicates fishing localities from where skipjack tuna stomachs were obtained. Hatched area shows larval occurrence (Matsuura 1982).

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038; present address: School of Fisheries, University of Washington, Seattle, WA 98195.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

Dragovich (1969) reviewed existing information on the food habits of Atlantic skipjack tuna. Since that time food habits have also been reported in studies by Dragovich (1970) and Dragovich and Potthoff (1972) for skipjack from the East and West Atlantic and by Batts (1972) for skipjack in North Carolina waters. Zavala-Camin (1981) examined predator-prey interactions of fishes, including skipjack captured north of the area in this study.

The primary objective of this study was to discover if skipjack tuna feed upon their young. The presence of juveniles in bait-caught skipjack stomachs would verify the study area as a spawning-rearing ground. Knowledge of the prey and their relative importance also contributes to the understanding of prey-predator interactions, which affect population distributions and fluctuations.

MATERIALS AND METHODS

Stomach samples for this study were collected on a monthly basis from October 1981 to December 1982 from skipjack tuna caught off Rio de Janeiro (Fig. 1). National Marine Fisheries Service (NMFS) personnel collected stomachs from frozen fish transhipped to Puerto Rico, and Superintendencia do Desenvolviemento da Pesca (SUPEDE) personnel sampled fish landed locally in Rio de Janeiro. Fish from the Puerto Rican source were caught within 1 mo prior to sampling; fish from the Brazilian source were sampled 3 to 5 d after the recorded catch date. The sampling design required collecting about 15 stomachs from each 10 cm length group, measured to the nearest cm per month. However, the number of stomachs collected was dependent on the catch-size distribution. Once the stomach was removed from the fish, it was preserved in 10% buffered Formalin[2] and shipped to the Southwest Fisheries Center (SWFC) for analysis.

Stomachs were examined from 1,041 fish between 44 and 81 cm fork length. In the laboratory each stomach was opened. The volume of the food bolus was measured, and the contents were identified to the lowest possible taxon. The taxonomic groupings were then measured by volumetric displacement, and the individuals counted. Whole undigested fish were identified by comparing external characters with those described in published keys or with identified museum specimens from Scripps Institution of Oceanography, La Jolla, CA. Digested animals, particularly juvenile scombrids, were identified by vertebral, gill raker, and fin ray counts, as well as other skeletal characteristics, described by Potthoff and Richards (1970), Miller and Jorgenson (1973), and other published keys. Cephalopods were identified by comparing beak characters with published illustrations, descriptions, and keys (see Wolff 1981). Crustaceans and other invertebrates were identified by specialists from Scripps Institution of Oceanography and SWFC.

The occurrence of bait in the stomachs may have biased the relative importance of fish in the diet. The bait primarily consisted of *Sardinella brasiliensis*, *Harengula jaguana*, and *Engraulis anchoita*; however, other fish families may have been included in the captured bait. The sardines were readily identifiable from their external characters and usually were undigested. The anchovies, in contrast, were often quite digested, creating difficulties in identification. Gary Nelson[3] nevertheless was able to verify these fish as *Engraulis anchoita*. Although the least digested item in the stomach was usually the last meal (bait), stomachs were removed from a few days to 1 mo after capture, and presumably postmortem digestion occurred. As a result, the degree of digestion was not a reliable indication of distinguishing bait from natural prey. The time required for complete gastric evacuation of smelt fed to skipjack tuna is estimated to be 12 h (Magnuson 1969). Although the bait was captured in nets from bays and estuaries (Rinaldo[4]), Matsuura et al. (1978, 1981) have confirmed that a spawning stock of *E. anchoita* does exist in waters inhabited by skipjack tuna. It is unlikely that the sardines served as prey for skipjack. However, I could not distinguish between *E. anchoita* consumed as natural food and as bait. Therefore, although these species were considered bait, some may have been ingested as natural food. Bait was not considered prey, and stomachs containing only these species were treated as empty.

Two methods of analysis were employed to rank the food items in terms of availability and importance to the skipjack tuna:

1) An index of relative importance (*IRI*) was calculated for each prey type in terms of numbers, volumes, and frequencies (Pinkas et al. 1971):

$$IRI = (N + V)F$$

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]G. J. Nelson, Department of Ichthyology, American Museum of Natural History, New York, NY 10024, pers. commun., May 1982.

[4]R. R. Rinaldo, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun., June 1982.

where N = numerical percentage
V = volumetric percentage
F = frequency of occurrence percentage.

2) The mean volumetric ratio measurement (*MVRM*) was used to illustrate the biomass importance of prey items without the numeric exaggeration implicit in the *IRI* (John Hedgepeth[5]). The *MVRM* was calculated from the volumetric analysis of individual stomachs with each prey item contributing to the total stomach volume. *MVRM* for each food type is expressed as

$MVRM = \bar{r}_j \times 100$ = mean volumetric percentage of prey j to the total volume of n stomachs

where N = number of stomachs in a given strata
V_{ij} = volume of prey type j in stomach i

$$V_i = \sum_{j=1}^{6} V_{ij} = \text{total volume of stomach } i$$

$$r_{ij} = \frac{V_{ij}}{V_i} = \text{ratio of prey } j \text{ to the total volume of stomach } i$$

$$\bar{r}_j = \frac{\sum_{i=1}^{n} r_{ij}}{n} = \text{mean volumetric ratio of prey } j \text{ to the total volume of } n \text{ stomachs.}$$

Both the *IRI* and the *MVRM*, which examine different aspects of the diet, were used to evaluate seasonal variations in skipjack tuna food habits. The *IRI* presents a biased estimate caused by the numerical percentage; the relative importance of small numerous organisms, like euphausiids, is exaggerated in the *IRI* because of their high numbers, when actually they may represent the same food value as a few large fish. The *MVRM* is an expression of frequency of occurrence and volume without a numeric bias, but does not provide any information on prey abundance. The *IRI* contains information on the availability of the prey in the environment in terms of numbers, while the *MVRM* provides an indication of its energetic importance to the fish.

The *MVRM*s were stratified by fish length and annual quarter (Fig. 2), and tested with the Kruskal-Wallis nonparametric one-way analysis of variance to evaluate differences in diet with changes in size.

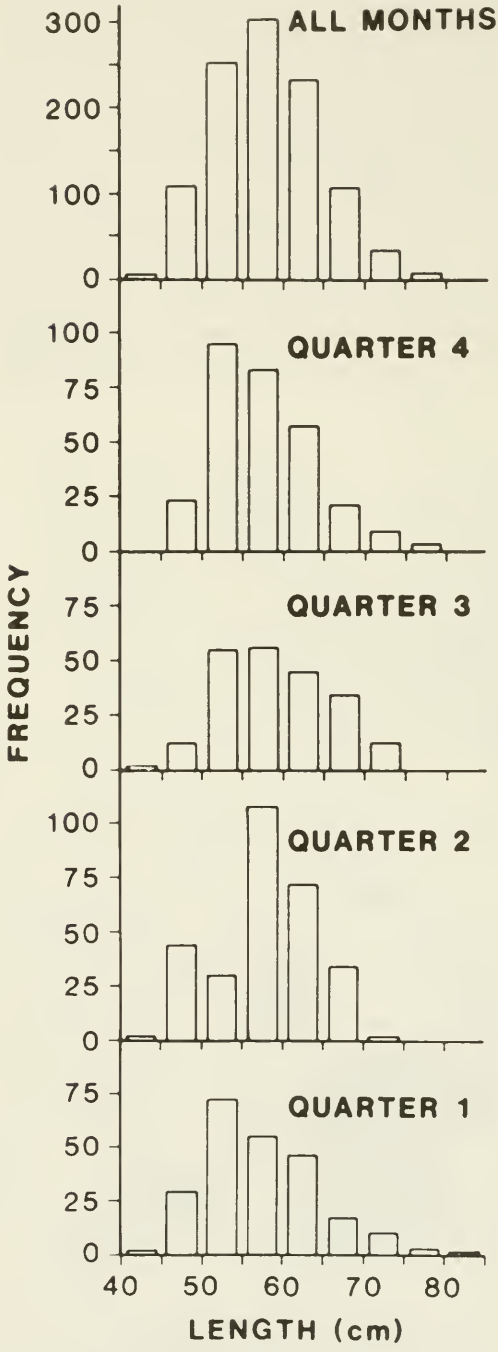


FIGURE 2.—Length-frequency distribution of skipjack tuna from which stomachs were collected.

[5]J. B. Hedgepeth, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun., April 1982.

RESULTS

Food Composition

Of the 1,041 stomachs that were examined, 436 were empty. The mean volume of food in all stomachs examined was 36.9 mL, of which 18.9 mL was bait and 18.0 mL was prey. A complete list of the stomach contents in terms of numbers, volume, and frequency is presented in Appendix Table 1. No larval or juvenile skipjack were found in the stomach contents. Overall contributions of each category are presented in Figure 3.

In terms of the *MVRM*, the gonostomatid *Maurolicus muelleri* was the major prey item (*MVRM* = 26.7%). The euphausiid *Euphausia similis*, with the highest *IRI*, was also important (*IRI* = 1,998). These items were major constituents of the diet throughout the year. Other important fishes in terms of both the

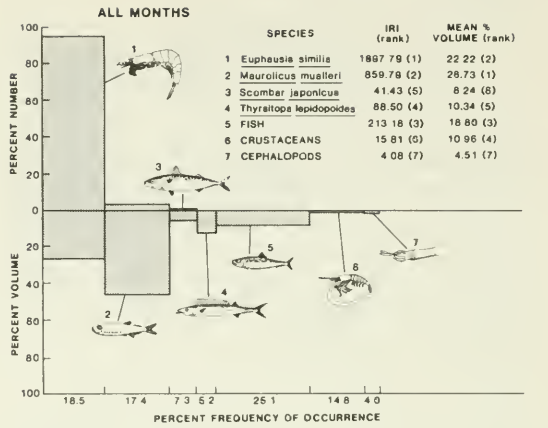
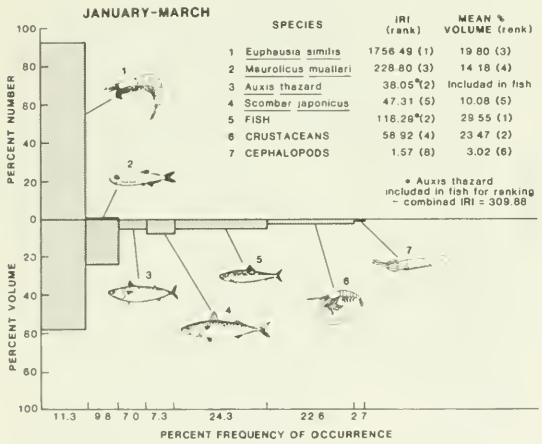
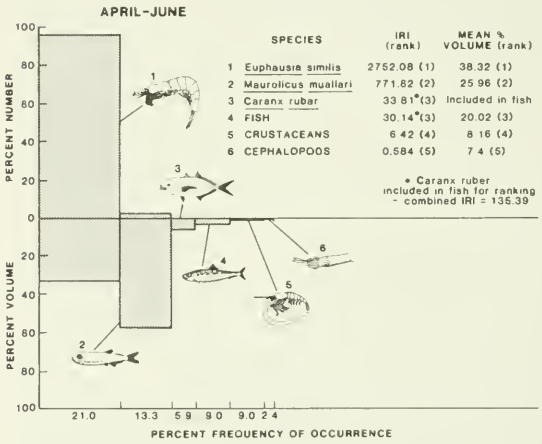
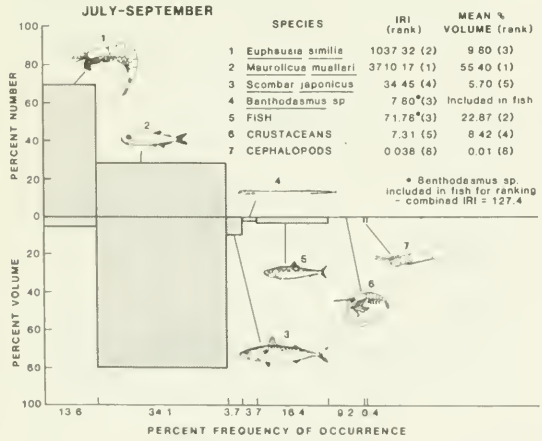


FIGURE 3.–Index of relative importance (IRI) plots for selected food items of skipjack tuna caught during 1982. The food categories are ranked in terms of IRI and MVRM.







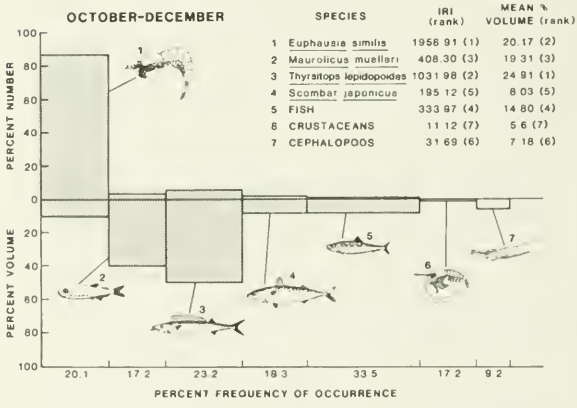


FIGURE 4.–Index of relative importance (IRI) plots for selected food items of skipjack tuna. The complete data are divided into four 3-mo quarters (I-IV). The food categories are ranked in terms of IRI and mean percent volume.

IRI and *MVRM* were chub mackerel, *Scomber japonicus*, and *Thyrsitops lepidopoides*[6] (Fig. 3). Crustaceans other than *E. similis* occurred frequently in the stomachs (F = 22.6%), but as a relatively low percentage of the total volume (V = 2.0%). Cephalopods were usually insignificant in the diet (see below). Pteropods, siphonophores, beetles, rocks, and unidentified materials were the constituents of the miscellaneous category (App. Table 1).

Seasonal Variations

The data were divided into four quarters: January-March 1982 (I), April-June 1982 (II), July-September 1982 (III), October-December 1981 and 1982 (IV). The results (App. Tables 2-6) are illustrated in Figures 4 and 5 both with the *IRI* and the *MVRM* of dominant food items in each quarter. Note that items important in one quarter may be negligible or absent in another. When evaluated in terms of *MVRM*, the prey ranks sometimes did not coincide with those determined by the *IRI* (Figs. 4, 5). Based on the *IRI*, *E. similis* was the dominant food in the first quarter, followed by other fish and *M. muelleri* (Fig. 4). According to the *MVRM*, other fishes, other crustaceans, and *E. similis* were ranked first, second, and third in importance, respectively. The importance of *E. similis* in this quarter based on the *IRI* was exaggerated by their high frequencies of occurrence. *Scomber japonicus* and frigate tuna, *Auxis thazard*, were secondary in importance to *M. muelleri* as the main fish species consumed.

The rankings of the food categories in the second quarter were the same for both the *IRI* and the *MVRM* (Fig. 4). *Euphausia similis* and *M. muelleri* were the dominant food items, followed by *Caranx ruber*.

[6]Identified by Y. Matsuura, Universidade de São Paulo, Instituto Oceanografico, São Paulo, Brazil, October 1984.

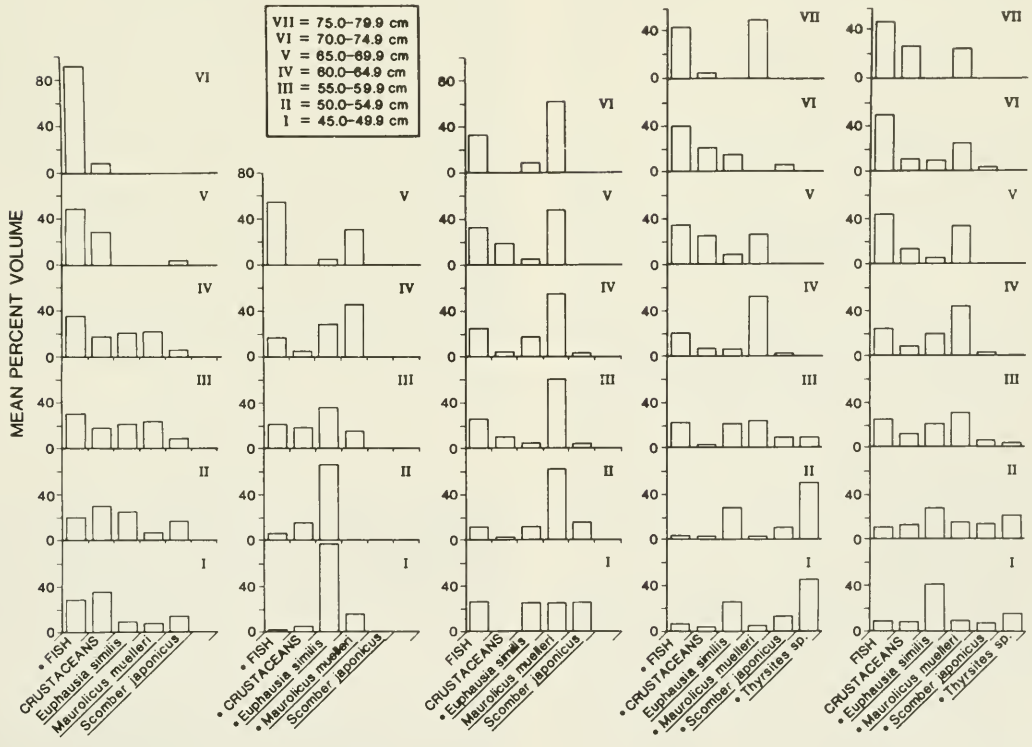


FIGURE 5.—Relative importance based on mean volumetric ratio of selected food items for skipjack tuna grouped by length for each quarter (I-IV) and all months. * indicates a significant difference ($P < 0.05$) in the mean percent volume of that food item by length when tested with the Kruskal-Wallis nonparametric one-way analysis of variance.

The principal food item in the third quarter based on both measurements was *M. muelleri* (Fig. 4). The ranks for the other items did not correspond. *Euphausia similis* was second in importance according to the *IRI*, but ranked third next to other fish based on the *MVRM*. *Scomber japonicus* and *Benthodesmus* sp. were the predominant species consumed in the fish category.

The *IRI* and *MVRM* ranks in the fourth quarter corresponded with the exception of the principal prey type (Fig. 4). Again, *E. similis* ranked first according to the *IRI*, but *Thyrsitops lepidopoides* was the primary food item based on the *MVRM*. Cephalopods, mainly *Argonauta* sp., were consumed in significant proportions in this quarter (*IRI* = 31.7, *MVRM* = 7.2%).

In summary, *M. muelleri* and *E. similis* predominated in the skipjack tuna diet during all quarters (Fig. 3). With the exception of the second quarter, *S. japonicus* was an important food item. *Benthodesmus* sp., *C. ruber*, *A. thazard*, as well as the cephalopod, *Argonauta* sp., also proved important in specific quarters. The importance of *T. lepidopoides* in Figure 3 was exaggerated by its predominance in the fourth quarter.

Variations with Size

As might be expected, basic dietary changes occur as the skipjack tuna grow. Nakamura (1965), Alverson (1963), Batts (1972), Dragovich and Potthoff (1972), and Wilson (1982) observed a decrease in the relative importance of crustaceans and an increasing importance of fish in the diet, as the skipjack size increased.

To evaluate the relationship between size and food habits, the skipjack were arbitrarily divided into seven 5 cm groups (Fig. 2). For each prey category the *MVRM*s were stratified by size group and quarter (App. Tables 6-10, Fig. 5). Trends reported in the results for length groups > 70 cm may not represent feeding habits of skipjack tuna from the study area because the sample sizes were too small (Fig. 2, App. Table 6).

There were no significant differences ($P < 0.05$) in diet and size in the first quarter except in the amount of other fish consumed (Fig. 5, App. Table 7). The *MVRM* of this category increased from 28.7% in skipjack 45.0-49.9 cm to 91.7% in fish 75.0-79.9 cm.

In the second quarter the proportions of other fish, other crustaceans, *E. similis*, and *M. muelleri* significantly changed with size (Fig. 5, App. Table 8). The larger skipjack tuna ate more fish (*MVRM* = 1.7% in the 45.0-49.9 cm size class to *MVRM* = 54.1% in the 75.0-79.9 cm size class) and more *M. muelleri* (*MVRM* = 15.4% to *MVRM* = 30.3%) than the smaller skipjack. As their size increased, skipjack decreased their consumption of *E. similis* from MVRM = 76.9% to *MVRM* = 4.5%. There was a significant difference between size classes ($P < 0.05$) in the *MVRM* of other crustaceans in the diet, but this difference seemed uncorrelated to increases in size.

In the third quarter there were no significant differences in the diet with increasing size except that the *MVRM* of *E. similis* decreased from 25.0% to 8.0% (Fig. 5, App. Table 9).

Thyrsitops lepidopoides was eaten by the smaller skipjack (45-59.9 cm) only in the fourth quarter (Fig. 5, App. Table 10). Although there were significant differences ($P < 0.05$) in the diets between the seven size groups during this period, these differences again seemed unrelated to increasing size.

In summary, when the data on *T. lepidopoides* were included with the rest of the fish data, there were no significant differences between size groups in the proportions of other fish consumed throughout the year (Fig. 5, App. Table 6). The *MVRM* of *E. similis* in the diet decreased from 42.5% in skipjack tuna 45.0-49.9 cm to 0.0% in skipjack 75.0-79.9 cm. There were significant differences in the percentages of *M. muelleri* and *S. japonicus* between the size classes. There were no significant differences in the *MVRM* of other crustaceans with changes in size.

As reported in the studies of the food habits of skipjack tuna referred to above, the stomach contents of skipjack from this area indicated the basic dietary changes associated with increasing size: a significant decrease in the proportion of *E. similis*, the predominant crustacean prey, and an increase in proportion of *M. muelleri*, the predominant fish prey.

DISCUSSION

Several studies have reported that skipjack tuna feed predominantly on euphausiids and gonostomatids. Dragovich and Potthoff (1972) reported that the gonostomatid *Vinciguerria nimbaria* contributed 44.7% by volume to the diet of skipjack tuna from the Gulf of Guinea. Zavala-Camin (1981) reported *M. muelleri* and euphausiids as dominant food items in 36 stomachs of skipjack caught off Brazil. Alverson (1963) reported skipjack tuna captured in the eastern tropical Pacific fed primarily on euphausiids (47% by volume, in 37% of the stomachs), followed in importance by the gonostomatid *Vinciguerria lucetia* (10% by volume). The abundance of euphausiids in

the stomachs of skipjack, compared with larger scombrids, may be a result of smaller gill raker gaps in skipjack (Magnuson and Heitz 1971).

The importance of other fishes as food for western Atlantic skipjack tuna observed in this study has been previously reported. Dragovich (1970) found a predominance of fish in the stomachs of skipjack caught off the eastern United States and the Caribbean. Suarez-Caabro and Duarte-Bello (1961) found that fishes constituted 75% of the total volume, followed by squid (23%) and crustaceans (2%), in the stomachs of Cuban skipjack. Zavala-Camin (1981) observed that fish constituted 38.9%, crustaceans 22.2%, and mollusks 2.8% of the total stomach volume of Brazilian skipjack.

CONCLUSIONS

The multiplicity of prey found in this as well as other studies indicates that tunas are perhaps nonselective feeders, and stomach contents are probably determined by prey availability (Hotta and Ogawa 1955; Alverson 1963; Batts 1972; Perrin et al. 1973; Argue et al. 1983). Therefore, if the larval and juvenile skipjack were available in significant numbers, then one would expect them to occur in the diet of the adults.

Their absence in the diet was caused by two possible results. First, the young remained among the unidentified portion of the stomach contents; however, skipjack tuna have distinctive vertebral characteristics which were probably not discounted in the analysis (Potthoff and Richards 1970). Second, the adults did not spawn in the study area. Young skipjack should be found in the stomach contents of spawning adults (Argue et al. 1983). Goldberg and Au[7] found no evidence of spawning in skipjack collected from the Brazilian fishery. These results are consistent with the absence of larval and juvenile skipjack in the diet of the adults in this study.

The southernmost distribution boundary for larval skipjack tuna is the 24°C surface isotherm (Argue et al. 1983). Matsuura (1982) found no larval skipjack in ichthyoplankton surveys south of lat. 21°S in this area, where temperatures range from 21° to 24°C (Evans et al. 1981).

These results are consonant with those of Argue et al. (1983); juvenile skipjack tuna were absent from samples of adult stomachs taken in subtropical south Pacific waters. The adult skipjack in this investigation did not feed on their young. The absence of cannabilism suggests that larvae and juveniles were not significantly abundant to serve as forage of the adults, and therefore probably do not occur in this cooler southern water.

ACKNOWLEDGMENTS

I wish to thank Ronald Rinaldo for organizing the collection of stomachs from skipjack tuna landed in Puerto Rico and Brazil. Silvio Jablonski (SUDEPE, Brazil), Eugene Holzapfel (NMFS, Puerto Rico), and their employees were responsible for the collection and shipment of the skipjack tuna stomachs.

Gareth Nelson, Richard Rosenblatt, Kurt Schaeffer, and Betsy Stevens assisted in the identification of the fishes. The euphasiid was identified by Edward Brinton. Robert Olson assisted in the identification of cephalopod beaks. Angeles Alvarino assisted in the identification of other invertebrates.

Thanks to Andrew Dizon, John Graves, Ronald Rinaldo, Robert Olson, and Kurt Schaeffer for their criticisms and suggestions in reviewing this paper.

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APPENDIX

APPENDIX TABLE 1.—List of prey items and other ingested materials found in the stomachs of 1,041 skipjack tuna caught off southern Brazil, from October 1981 to December 1982.

	Numbers		Volume		Occurrence	
Prey items	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	12.0	0.003	4.5	0.024	6.0	0.576
Mysidacea						
Eucopiidae	220.0	0.057	42.4	0.226	22.0	2.113
Lophogastridae	24.0	0.006	1.7	0.009	3.0	0.288
Isopoda	1.0	0.000	0.1	0.001	1.0	0.096
Flabellifera	7.0	0.002	2.1	0.011	7.0	0.672
Amphipoda	22.0	0.006	1.5	0.008	2.0	0.192
Gammaridea	16.0	0.004	5.1	0.027	10.0	0.961
Euphausiidae	139.0	0.036	3.9	0.021	15.0	1.441
Euphausia sp.	50.0	0.013	0.6	0.003	1.0	0.096
Euphausia similis	368,632.0	94.785	4,895.3	26.122	172.0	16.523
Stylocheiron sp.	1.0	0.000	0.3	0.002	1.0	0.096
Caridea	3.0	0.001	2.3	0.012	3.0	0.288
Macrura						
Scyllaridae	1.0	0.000	0.2	0.001	1.0	0.096
Unid. Phyllosoma larvae	1.0	0.000	0.1	0.001	1.0	0.096

APPENDIX TABLE 1.—*Continued.*

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Brachyura	5.0	0.001	0.7	0.004	1.0	0.096
Portunidae	1.0	0.000	0.1	0.001	1.0	0.096
Unid. megalops	102.0	0.026	32.0	0.171	27.0	2.594
Unid. zooea	555.0	0.143	30.2	0.161	24.0	2.305
Unid. Decapoda	7.0	0.002	0.6	0.003	2.0	0.192
Unid. Crustacea	96.0	0.025	11.0	0.059	26.0	2.498
Mollusca						
Gastropoda	1.0	0.000	0.1	0.001	1.0	0.096
Cavolina sp.	101.0	0.026	6.0	0.032	7.0	0.672
Cephalopoda						
Teuthoidea	4.0	0.001	26.0	0.139	4.0	0.384
Thysanoteuthidae	2.0	0.001	10.0	0.053	1.0	0.096
Ommastrephidae	35.0	0.009	55.1	0.294	18.0	1.729
Loliginidae	2.0	0.001	10.5	0.056	2.0	0.192
Histioteuthidae	1.0	0.000	1.0	0.005	1.0	0.096
Onychoteuthidae	13.0	0.003	6.0	0.032	2.0	0.192
Octopoda						
Argonautidae						
Argonauta sp.	20.0	0.005	75.9	0.405	11.0	1.057
Unid. Cephalopoda	4.0	0.001	1.3	0.007	3.0	0.288
Insecta						
Coleoptera	2.0	0.001	2.0	0.011	2.0	0.192
Siphonophora	1.0	0.000	0.9	0.005	1.0	0.096
Algalmidae	8.0	0.002	6.6	0.035	8.0	0.768
Pisces						
Gonostomatidae						
Maurolicus muelleri	13,438.0	3.455	8,619.3	45.994	181.0	17.387
Synodontidae	8.0	0.002	16.0	0.085	3.0	0.288
Paralepididae	1.0	0.000	0.5	0.003	1.0	0.096
Myctophidae	43.0	0.011	62.3	0.332	5.0	0.480
Exocoetidae	2.0	0.001	2.0	0.011	2.0	0.192
Exocoetus volitans	1.0	0.000	56.0	0.299	1.0	0.096
Scomberesocidae						
Scomberesox saurus	8.0	0.002	105.0	0.560	6.0	0.576
Belonidae	2.0	0.001	5.0	0.027	2.0	0.192
Macrorhamphosidae	5.0	0.001	6.9	0.037	4.0	0.384
Sygnathidae	1.0	0.000	1.0	0.005	1.0	0.096
Holocentridae	3.0	0.001	4.0	0.021	1.0	0.096
Holocentrus sp.	3.0	0.001	9.0	0.048	1.0	0.096
Carangidae	1.0	0.000	1.0	0.005	1.0	0.096
Selene vomer	8.0	0.002	17.0	0.091	8.0	0.768
Decapterus punctatus	2.0	0.001	46.0	0.245	2.0	0.192
Caranx ruber	70.0	0.018	360.0	1.921	17.0	1.633
Mullidae	11.0	0.003	25.0	0.133	6.0	0.576
Scombridae	16.0	0.004	2.5	0.013	3.0	0.288
Auxis thazard	474.0	0.122	223.7	1.194	23.0	2.209
Scomber japonicus	1,474.0	0.379	978.7	5.223	77.0	7.397
Sarda sarda	81.0	0.021	127.0	0.678	8.0	0.768
Gempylidae	176.0	0.045	100.7	0.537	20.0	1.921
Thyrsitops lepidopoides	2,617.0	0.673	2,348.4	12.532	54.0	5.187
Trichiuridae	11.0	0.003	12.0	0.064	4.0	0.384
Benthodesmus sp.	19.0	0.005	80.9	0.432	8.0	0.768
Unid. Perciforms	24.0	0.006	63.7	0.340	16.0	1.537
Balistidae	1.0	0.000	5.0	0.027	1.0	0.096
Monacanthidae	27.0	0.007	19.8	0.106	19.0	1.825
Ostraciidae	1.0	0.000	0.5	0.003	1.0	0.096
Molidae						
Ranzania sp.	3.0	0.001	13.0	0.069	1.0	0.096
Triglidae	1.0	0.000	1.0	0.005	1.0	0.096
Peristedion sp.	1.0	0.000	1.0	0.005	1.0	0.096
Unid. fish	289.0	0.074	163.5	0.872	94.0	9.030
Unid. material	1.0	0.000	26.4	0.141	5.0	0.480
Empty					436.0	41.882
Total	388,912.0		18,739.9		1,041.0	

APPENDIX TABLE 2.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter I.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Mysidacea						
Eucopiidae	112.0	0.0076	9.3	0.253	8.0	2.658
Lophogastridae	19.0	0.013	1.5	0.041	2.0	0.664
Isopoda	1.0	0.001	0.1	0.003	1.0	0.332
Flabellifera	1.0	0.001	0.1	0.003	1.0	0.332
Amphipoda	20.0	0.014	0.5	0.014	1.0	0.332
Euphausiidae	49.0	0.033	2.3	0.063	4.0	1.329
Euphausia similis	144,070.0	97.624	2,125.9	57.878	34.0	11.296
Caridea	1.0	0.001	0.5	0.014	1.0	0.332
Brachyura						
Unid. megalops	80.0	0.054	22.6	0.615	17.0	5.648
Unid. zooea	549.0	0.372	28.6	0.779	19.0	6.312
Unid. Decapoda	4.0	0.003	0.1	0.003	1.0	0.332
Unid. Crustacea	47.0	0.032	8.3	0.226	13.0	4.319
Mollusca						
Gastropoda						
Pteropoda						
Cavolina	68.0	0.046	2.2	0.060	1.0	0.332
Cephalopoda						
Teuthoidea	2.0	0.001	2.0	0.054	2.0	0.664
Thysanoteuthidae	2.0	0.001	10.0	0.272	1.0	0.332
Ommastrephidae	5.0	0.003	1.1	0.030	2.0	0.664
Loliginidae	1.0	0.001	8.0	0.218	1.0	0.332
Octopoda						
Argonautidae						
Argonauta sp.	2.0	0.001	0.3	0.008	2.0	0.664
Insecta						
Coleoptera	1.0	0.001	1.0	0.027	1.0	0.332
Pisces						
Gonostomatidae						
Maurolicus muelleri	1,346.0	0.912	838.0	22.815	29.0	9.635
Belonidae	1.0	0.001	3.0	0.082	1.0	0.332
Holocentridae	3.0	0.002	4.0	0.109	1.0	0.332
Carangidae						
Selene vomer	6.0	0.004	9.0	0.245	6.0	1.993
Mullidae	2.0	0.001	8.0	0.218	1.0	0.332
Scombridae	15.0	0.010	1.5	0.041	2.0	0.664
Auxis thazard	427.0	0.289	189.7	5.165	21.0	6.977
Scomber japonicus	504.0	0.342	225.2	6.131	22.0	7.309
Gempylidae	76.0	0.051	48.5	1.320	11.0	3.654
Unid. Perciforms	9.0	0.006	7.0	0.191	5.0	1.661
Monacanthidae	13.0	0.009	9.5	0.259	8.0	2.658
Ostraciidae	1.0	0.001	0.5	0.014	1.0	0.332
Triglidae	1.0	0.001	1.0	0.027	1.0	0.332
Peristedion sp.	1.0	0.001	1.0	0.027	1.0	0.332
Unid. fish	137.0	0.093	76.5	2.083	35.0	11.628
Unid. material	1.0	0.001	26.3	0.716	4.0	1.329
Total	147,577.0		3,673.1		301.0	

APPENDIX TABLE 3.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter II.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	1.0	0.001	1.0	0.016	1.0	0.345
Mysidacea						
Eucopiidae	97.0	0.055	31.9	0.508	9.0	3.103
Lophogastridae	5.0	0.003	0.2	0.003	1.0	0.345
Isopoda						
Flabellifera	2.0	0.001	1.5	0.024	2.0	0.690
Amphipoda	2.0	0.001	1.0	0.016	1.0	0.345
Gammaridea	6.0	0.003	0.4	0.006	3.0	1.034
Euphausiidae	2.0	0.001	0.2	0.003	2.0	0.690
Euphausia similis	171,843.0	97.352	2,104.3	33.485	61.0	21.034
Caridea	1.0	0.001	0.8	0.013	1.0	0.345
Macrura						
Scyllaridae	1.0	0.001	0.2	0.003	1.0	0.345
Brachyura						
Unid. megalops	1.0	0.001	0.5	0.008	1.0	0.345
Unid. zooea	1.0	0.001	0.2	0.003	1.0	0.345
Unid. Decapoda	3.0	0.002	0.5	0.008	1.0	0.345
Unid. Crustacea	30.0	0.017	1.2	0.019	2.0	0.690
Mollusca						
Gastropoda						
Pteropoda						
Cavolina sp.	33.0	0.019	3.8	0.060	6.0	2.069
Cephalopoda						
Teuthoidea						
Ommastrephidae	6.0	0.003	8.5	0.135	5.0	1.724
Onychoteuthidae	13.0	0.007	6.0	0.095	2.0	0.690
Siphonophora						
Algalmidae	8.0	0.005	6.6	0.105	8.0	2.759
Pisces						
Gonostomatidae						
Maurolicus muelleri	4,287.0	2.429	3,548.0	56.458	38.0	13.103
Synodontidae	8.0	0.005	16.0	0.255	3.0	1.034
Myctophidae	24.0	0.014	61.3	0.975	4.0	1.379
Sygnathidae	1.0	0.001	1.0	0.016	1.0	0.345
Carangidae						
Selene vomer	2.0	0.001	8.0	0.127	2.0	0.690
Decapterus punctatus	2.0	0.001	46.0	0.732	2.0	0.690
Caranx ruber	70.0	0.040	360.0	5.729	17.0	5.862
Scombridae						
Auxis thazard	46.0	0.026	30.0	0.477	1.0	0.345
Scomber japonicus	8.0	0.005	6.0	0.095	2.0	0.690
Unid. Perciforms	1.0	0.001	12.0	0.191	1.0	0.345
Balistidae	1.0	0.001	5.0	0.080	1.0	0.345
Monacanthidae	4.0	0.002	4.1	0.065	3.0	1.034
Unid. fish	9.0	0.005	18.1	0.288	6.0	2.069
Total	176,518.0		6,284.3		290.0	

APPENDIX TABLE 4.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter III.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Mysidacea						
Eucopiidae	10.0	0.046	0.8	0.020	4.0	1.843
Isopoda						
Flabellifera	2.0	0.009	0.3	0.007	2.0	0.922
Euphausiidae	88.0	0.401	1.4	0.034	9.0	4.147
Euphausia sp.	50.0	0.228	0.6	0.015	1.0	0.461
Euphausia similis	15,414.0	70.236	196.3	4.796	30.0	13.825
Unid. Crustacea	5.0	0.023	0.4	0.010	4.0	1.843
Mollusca						
Cephalopoda						
Teuthoidea	1.0	0.005	3.0	0.073	1.0	0.461
Pisces						
Gonostomatidae						
Maurolicus muelleri	6,239.0	28.429	3,289.2	80.369	74.0	34.101
Exocoetidae	2.0	0.009	2.0	0.049	2.0	0.922
Exocoetus volitans	1.0	0.005	56.0	1.368	1.0	0.461
Macrorhamphosidae	2.0	0.009	2.9	0.071	2.0	0.922
Carangidae	1.0	0.005	1.0	0.024	1.0	0.461
Mullidae	6.0	0.027	9.0	0.220	3.0	1.382
Scombridae						
Scomber japonicus	45.0	0.205	374.0	9.138	8.0	3.687
Sarda sarda	6.0	0.027	4.0	0.098	2.0	0.922
Trichiuridae	11.0	0.050	12.0	0.293	4.0	1.843
Benthodesmus sp.	19.0	0.087	80.9	1.977	8.0	3.687
Unid. Perciforms	4.0	0.018	35.0	0.855	3.0	1.382
Monacanthidae	1.0	0.005	1.0	0.024	1.0	0.461
Unid. fish	39.0	0.178	22.8	0.557	21.0	9.677
Total	21,946.0		4,092.6		217.0	

APPENDIX TABLE 5.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter IV.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	11.0	0.026	3.5	0.075	5.0	2.146
Mysidacea						
Eucopiidae	1.0	0.002	0.4	0.009	1.0	0.429
Isopoda						
Flabellifera	2.0	0.005	0.2	0.004	2.0	0.858
Amphipoda						
Gammaridea	10.0	0.023	4.7	0.100	7.0	3.004
Euphausiidae						
Euphausia similis	37,305.0	87.017	468.8	9.996	47.0	20.172
Stylocheiron sp.	1.0	0.002	0.3	0.006	1.0	0.429
Caridea	1.0	0.002	1.0	0.021	1.0	0.429
Macrura						
Scyllaridae						
Unid. Phyllosoma larvae	1.0	0.002	0.1	0.002	1.0	0.429
Brachyura	5.0	0.012	0.7	0.015	1.0	0.429
Portunidae	1.0	0.002	0.1	0.002	1.0	0.429
Unid. megalops	21.0	0.049	8.9	0.190	9.0	3.863
Unid. zooea	5.0	0.012	1.4	0.030	4.0	1.717
Unid. Crustacea	14.0	0.033	1.1	0.023	7.0	3.004
Mollusca						
Gastropoda						
Pteropoda						
Cavoliniidae	1.0	0.002	0.1	0.002	1.0	0.429
Cephalopoda						
Teuthoidea	1.0	0.002	21.0	0.448	1.0	0.429
Ommastrephidae	24.0	0.056	45.5	0.970	11.0	4.721
Loliginidae	1.0	0.002	2.5	0.053	1.0	0.429
Histioteuthidae	1.0	0.002	1.0	0.021	1.0	0.429
Octopoda						
Argonautidae						
Argonauta sp.	18.0	0.042	75.6	1.612	9.0	3.863
Unid. Cephalopoda	4.0	0.009	1.3	0.028	3.0	1.288
Insecta						
Coleoptera	1.0	0.002	1.0	0.021	1.0	0.429
Siphonophora	1.0	0.002	0.9	0.019	1.0	0.429
Pisces						
Gonostomatidae						
Maurolicus muelleri	1,566.0	3.653	944.1	20.130	40.0	17.167
Paralepididae	1.0	0.002	0.5	0.011	1.0	0.429
Myctophidae	19.0	0.044	1.0	0.021	1.0	0.429
Scomberesocidae						
Scomberesox saurus	8.0	0.019	105.0	2.239	6.0	2.575
Belonidae	1.0	0.002	2.0	0.043	1.0	0.429
Macrorhamphosidae	3.0	0.007	4.0	0.085	2.0	0.858
Holocentridae						
Holocentrus sp.	3.0	0.007	9.0	0.192	1.0	0.429
Mullidae	3.0	0.007	8.0	0.171	2.0	0.858
Scombridae	1.0	0.002	1.0	0.021	1.0	0.429
Auxis thazard	1.0	0.002	4.0	0.085	1.0	0.429
Scomber japonicus	917.0	2.139	373.5	7.964	45.0	19.313
Sarda sarda	75.0	0.175	123.0	2.623	6.0	2.575
Gempylidae	100.0	0.233	52.2	1.113	9.0	3.863
Thyrsitops lepidopoides	2,617.0	6.104	2,348.4	50.074	54.0	23.176
Unid. Perciforms	10.0	0.023	9.7	0.207	7.0	3.004
Monacanthidae	9.0	0.021	5.2	0.111	7.0	3.004
Molidae	1.0	0.001	0.5	0.014	1.0	0.332
Ranzania sp.	3.0	0.007	13.0	0.277	1.0	0.429
Unid. fish	104.0	0.243	46.1	0.983	32.0	13.734
Unid. material	0.0	0.000	0.1	0.002	1.0	0.429
Total	42,871.0		4,689.9		233.0	

APPENDIX TABLE 6.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for all months. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*	*Thyrsitops lepidopoides*
45.0-49.9(67)	9.51 ± 22.5	9.51 ± 25.4	42.50 ± 48.1	10.35 ± 29.5	8.57 ± 23.6	16.64 ± 36.4
50.0-54.9(155)	10.53 ± 27.7	12.62 ± 30.9	26.73 ± 43.6	13.99 ± 33.4	12.44 ± 29.5	20.05 ± 38.5
55.0-59.9(162)	24.81 ± 39.4	11.80 ± 29.5	20.40 ± 39.5	29.49 ± 43.6	5.62 ± 19.6	2.70 ± 14.2
60.0-64.9(147)	23.48 ± 39.2	8.03 ± 24.7	18.83 ± 36.5	42.90 ± 48.2	2.12 ± 12.2	—
65.0-69.9(55)	42.80 ± 47.6	12.43 ± 31.7	4.73 ± 18.7	32.18 ± 45.9	0.27 ± 2.0	—
70.0-74.9(13)	48.30 ± 48.1	9.88 ± 27.9	8.57 ± 21.9	23.36 ± 43.7	2.20 ± 79.2	—
75.0-79.9(4)	47.50 ± 55.0	27.50 ± 48.6	—	25.00 ± 50.0	—	—
Total (603)	18.80 ± 35.5	10.96 ± 28.6	22.22 ± 40.0	26.73 ± 42.8	6.24 ± 21.1	10.34 ± 27.9

APPENDIX TABLE 7.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter I. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(12)	28.70 ± 33.4	35.15 ± 42.5	9.18 ± 28.7	7.48 ± 25.9	13.89 ± 38.4
50.0-54.9(53)	19.87 ± 36.8	29.64 ± 43.5	24.48 ± 43.3	6.09 ± 19.6	16.12 ± 33.5
55.0-59.9(45)	30.23 ± 40.9	17.69 ± 33.9	20.81 ± 38.9	22.96 ± 38.1	7.98 ± 25.2
60.0-64.9(36)	34.79 ± 44.1	16.96 ± 35.4	20.14 ± 38.9	20.92 ± 40.1	19.84 ± 46.5
65.0-69.9(4)	48.61 ± 56.2	28.24 ± 47.9	—	—	3.71 ± 7.4
70.0-74.9(3)	91.67 ± 14.4	8.33 ± 14.4	—	—	—
75.0-79.9(2)	—	—	—	—	—
Total (155)	29.55 ± 41.0	23.47 ± 38.9	19.80 ± 38.9	14.18 ± 32.1	10.08 ± 27.3

APPENDIX TABLE 8.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter II. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(26)	1.65 ± 8.4	5.00 ± 20.3	76.92 ± 43.0	15.38 ± 36.8	—
50.0-54.9(12)	5.82 ± 11.5	14.72 ± 33.0	65.71 ± 48.6	—	—
55.0-59.9(35)	20.89 ± 38.7	18.13 ± 36.4	35.65 ± 49.9	14.71 ± 33.9	0.14 ± 0.80
60.0-64.9(45)	16.33 ± 36.2	4.67 ± 18.5	28.92 ± 45.7	45.54 ± 49.7	0.32 ± 2.1
65.0-69.9(23)	54.07 ± 49.1	—	4.49 ± 20.8	30.29 ± 46.8	—
Total (141)	20.02 ± 38.1	8.16 ± 25.2	38.32 ± 48.6	25.96 ± 43.3	0.14 ± 1.3

APPENDIX TABLE 9.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter III. Data are $\bar{r}$ ± SD with (*n*) in parentheses. Range is 0-100%.

Length cm (*n*)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(4)	25.81 ± 49.5	—	25.00 ± 50.0	24.19 ± 48.4	25.00 ± 50.0
50.0-54.9(27)	11.17 ± 32.0	1.24 ± 6.4	11.21 ± 32.0	61.56 ± 48.5	14.81 ± 36.2
55.0-59.9(36)	24.88 ± 41.3	9.22 ± 27.9	3.67 ± 16.2	59.05 ± 47.0	3.17 ± 16.8
60.0-64.9(31)	24.09 ± 40.5	3.39 ± 17.9	16.51 ± 29.9	53.76 ± 46.6	2.26 ± 12.6
65.0-69.9(17)	31.80 ± 46.4	17.65 ± 39.3	3.89 ± 9.8	46.67 ± 48.8	—
70.0-74.9(5)	31.27 ± 45.5	—	8.00 ± 17.9	60.73 ± 53.8	—
Total (120)	22.87 ± 40.1	6.42 ± 23.6	9.6 ± 25.5	55.40 ± 47.39	5.70 ± 22.7

APPENDIX TABLE 10.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter IV. Data are $\bar{x} \pm$ SD with (n) in parentheses. Range is 0-100%.

Length cm (n)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*	*Thyrsitops lepidopoides*
45.0-49.9(25)	5.86 ± 13.8	3.43 ± 11.0	25.49 ± 39.6	4.26 ± 16.9	12.30 ± 25.1	44.60 ± 48.4
50.0-54.9(63)	3.30 ± 13.4	2.77 ± 13.0	27.84 ± 43.4	2.91 ± 16.3	10.69 ± 25.1	49.33 ± 47.0
55.0-59.9(46)	22.45 ± 37.5	3.25 ± 15.3	21.48 ± 40.2	24.01 ± 42.9	9.40 ± 22.5	9.49 ± 25.7
60.0-64.9(35)	20.51 ± 35.4	7.29 ± 22.1	6.55 ± 19.5	52.48 ± 49.9	1.71 ± 85.6	—
65.0-69.9(11)	34.11 ± 44.1	24.59 ± 40.2	8.26 ± 27.4	25.45 ± 43.9	—	—
70.0-74.9(5)	39.31 ± 53.8	20.69 ± 44.4	14.29 ± 31.9	—	5.71 ± 12.8	—
75.0-79.9(2)	45.00 ± 63.6	5.00 ± 7.1	—	50.0 ± 70.7	—	—
Total (187)	14.80 ± 16.5	5.6 ± 19.5	29.17 ± 37.8	19.31 ± 38.9	8.03 ± 21.2	24.91 ± 27.7

STOMACH CONTENTS OF YOUNG SANDBAR SHARKS, *CARCHARHINUS PLUMBEUS*, IN CHINCOTEAGUE BAY, VIRGINIA[1]

ROBERT J. MEDVED,[2] CHARLES E. STILLWELL,[3] AND JOHN J. CASEY[3]

ABSTRACT

During the summer of 1983 the stomach contents of 414 sandbar sharks captured by gill nets, and rod and reel fishing gear in Chincoteague Bay, Virginia, were examined. The blue crab, *Callinectes sapidus*, occurred in 67.4% of the stomachs and Atlantic menhaden, *Brevoortia tyrannus*, occurred in 13.3% of the stomachs. Other species of small crustaceans and fishes were found in < 6.0% of the stomachs, and 17.9% of the stomachs were empty. Data collected concerning the amount, stage of digestion, and number of food items in the stomachs indicated that feeding occurred during relatively short periods of time separated by long periods during which food was digested and no additional food was consumed. Sharks caught in gill nets were found to be in various stages of the feeding cycle and were more representative of the entire population than those caught by rod and reel. In the stomachs of these sharks, crustaceans accounted for nearly twice as much of the mean weight of food as did fish. The mean quantity of food in the stomachs was 0.96% of body weight (BW) and the maximum quantity was 5.28% of BW. The quantity of food in all stomachs was significantly less than the estimated maximum stomach capacity (13.0% BW). Sharks caught between 0130 and 0430 were found to contain considerably more food in their stomachs than sharks caught during other times of the day. The data collected from this study when combined with information concerning gastric evacuation will provide the basis for food consumption estimates in this species.

Traditionally the management of commercially valuable fisheries has been based on single-species production models and the concept of maximum sustainable yield (Hennemuth 1979). Although generally accepted as an objective of management, the estimation and application of maximum sustainable yield have not provided satisfactory results and have, in fact, led to significant declines of some traditional and highly valued fisheries (Edwards and Hennemuth 1975; Hennemuth 1977; Holt and Talbot 1978). The poor results of single-species models in allocating fishing quotas may be due in part to the fact that they assume no interactions of the target species with other components of the ecosystem. In recent years it has become clear that this assumption is unrealistic and that variables such as competition, predation, and abiotic factors should be considered in any assessment of fishery productivity and potential yields to man. It has been pointed out (Gulland 1978, 1983; Mercer 1982) that the future success of our attempts at managing fishery resources will depend, to a large extent, on our ability to develop multispecies production models that adequately account for interactions among species. An important component of these models is predator-prey interactions. In fact, collection of data on the diets of the major predators is considered absolutely necessary for the progress of multispecies assessment techniques (Hennemuth 1980[4]; Mercer 1982). Considering their position as one of the most abundant apex predators in the sea, predation by sharks undoubtedly plays a major role in the exchange of energy in the marine environment. In fact, a study by Jones and Geen (1977) has indicated that the spiny dogfish, *Squalus acanthias*, in British Columbia waters annually consumes over 5 times the commercial catch of herring and up to 44% of the total stock. The impact that sharks have on commercial fisheries can only be determined by knowing the diversity of prey items and the biomass of each consumed. While numerous publications on sharks incorporate lists of items found in their stomachs, very little is known about daily ration and the amounts of food consumed annually.

[1]MARMAP Contribution No. MED/NEFC 84-02.

[2]University of Rhode Island, Graduate School of Oceanography, Narragansett, RI; present address: Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882.

[3]Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882.

[4]Hennemuth, R. C. 1980. Research needs for multispecies fisheries. Office of Technology Assessment Workshop, Seattle, WA., 21-23 April.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

In most investigations the food consumption of fishes has been studied by methods that involve laboratory techniques to estimate various parameters relating to growth, metabolism, digestion, and excretion (reviews by: Davis and Warren 1971; Mann 1978). These methods, however, are of limited value for fishes such as sharks that are difficult to maintain in captivity. An alternate method for determining food intake that can be applied to fishes in the wild has been successfully used in several studies (Bajkov 1935; Swenson and Smith 1973; Eggers 1977; Thorpe 1977; Elliott and Persson 1978; Jobling 1981; Stillwell and Kohler 1982; Durbin et al. 1983). This approach requires information concerning the quantity of food found in the stomachs of fishes sampled at regular intervals over 24-h periods and the rate at which food is evacuated from the stomach. The objective of the present study was to obtain the quantitative stomach content data needed to use this approach to estimate the daily food ration of the sandbar shark, *Carcharhinus plumbeus*. The sandbar shark was selected for this study because it is one of the few sharks for which gastric evacuation data are available (Medved in press). It is also an abundant, widely distributed shark (Springer 1960; Casey 1976) known to feed on commercially valuable species (Medved and Marshall 1981). In addition, it is a member of a large family of sharks (Carcharhinidae) and data collected for this species will provide the basis for making preliminary estimates of food consumption for the other members of the family.

METHODS

During the summer of 1983, young sandbar sharks were collected from Chincoteague Bay, VA, for stomach content analysis. The study area is located within the summer distribution of this species and supports a relatively large number of young sandbar sharks from early June through September. The bay is about 40 km long and 8 km wide at its widest point, and the average water depth is 2 m. A tidal inlet connects the bay with the Atlantic Ocean, and the tidal range varies from 0.75 to 1.50 m. The area is also characterized by strong tidal currents, vast salt marshes, and brackish to seawater salinities.

A 4.9 m outboard motor boat was used as a fishing platform, and sharks were caught using monofilament gill nets and rod and reel fishing gear. The gill nets were 91 m long, 1.8 m deep, and had a stretched mesh size of 10.8 cm. They were anchored at both ends and were buoyed so the foot rope touched the bottom. Net retrieval was made every 1 to 2 h. The fishing rods were equipped with Penn[5] reels of 3/0 size, and the terminal tackle consisted of two wire leaders, each with a 4/0 fishing hook baited with squid. The hooks were set 1 m off the bottom. Both types of gear were used during all hours of the day. Upon capture each shark was brought into the boat where it was sexed, measured, and weighed. The sharks were then cut open and the stomach contents were removed and stored on ice in plastic bags.

In the laboratory each food item was identified to species and a length measurement was made when possible. Each item in the stomach was also assigned a stage-of-digestion value ranging from 1 to 6 with a higher number indicating a greater extent of digestion. The stage-of-digestion scale was based on a gastric evacuation study (Medved in press) in which sandbar sharks were fed preweighed meals of either blue crab, *Callinectes sapidus*, or Atlantic menhaden, *Brevoortia tyrannus*, and were maintained in an enclosure constructed in the natural environment. The range of water temperatures in the enclosure (22.0°-30.0°C) was close to that recorded during the present study (20.0°-27.3°C). The sharks were sacrificed at various time intervals after feeding, and the food remains were weighed and described. The food item descriptions were used to arbitrarily establish six stages of digestion that were each one-sixth of the total evacuation time. Each stage of digestion was about 12 h long for crustacean prey and 15 h long for fish prey. After identification of food items and assignment of digestion values, the stomach contents of each shark were separated into fish and crustacean components that were weighed to 0.01 g after draining off excess water. Each sample was then dried at 80°C to constant weight (about 72 h) and again weighed to 0.01 g.

RESULTS

During the study 414 sharks were captured for stomach content analysis. The numbers of sharks caught by each fishing method and during various time periods of the day are summarized in Table 1. The number of male and female sharks collected was nearly equal (210 and 204 respectively), and they ranged in size from 40.0 to 80.0 cm fork length (FL) ($\bar{x}$ = 56.1, SD = 6.8). Body weights were obtained from 369 (89.1%) of these sharks, and ranged from 720.0 to 5,690.0 g ($\bar{x}$ = 1,885.5, SD = 738.8). The body weight of the sharks not weighed was estimated from a regression equation derived from the

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of sharks caught for stomach content analysis during different time intervals and by the two capture methods.

Time interval	Rod and reel	Gill net	Total
2230-0130	19	33	52
0130-0430	11	27	38
0430-0730	20	20	40
0730-1030	21	27	48
1030-1330	27	27	54
1330-1630	39	39	78
1630-1930	18	30	48
1930-2230	23	33	56
Total	178	236	414

animals that were measured and weighed: $Wt = 0.0123\ (FL)^{2.9577}$ ($n = 369$, $R^2 = 0.97$). Water temperature during the fishing periods ranged from 20.0° to 27.3°C ($n = 172$, $\bar{x} = 25.1$) but 90% of the temperatures were between 23.9° and 26.4°C.

Fifteen different food types were identified in the stomachs (Table 2). A relatively large number of stomachs ($n = 74$, 17.9%) were empty, and unidentifiable fish remains occurred in others ($n = 21$, 5.1%). The blue crab was the most frequently occurring food item and was found in 279 (67.4%) of the stomachs examined and in 82.1% of the stomachs containing food. Of the food remains that could be positively identified as individual blue crabs ($n = 309$), 88.0% of the crabs had recently molted and were soft. The crabs that could be measured ranged in size from 1.0 to 14.0 cm between the two points of the carapace ($n = 136$, $\bar{x} = 7.4$). Although exact numbers were difficult to determine, it appeared that less than half of the blue crabs were consumed whole. The only other prey frequently found was the Atlantic menhaden, which occurred in 55 (13.3%) of the stomachs examined and in 16.2% of the stomachs with food. Of the 61 cases where it was possible to determine if the fish was consumed whole or in part, 28 (45.9%) of the menhaden were whole and ranged in size from 5 to 10 cm total length (TL) ($\bar{x} = 7.3$). The estimated sizes of the partially eaten menhaden ranged from 5 to 17 cm TL ($\bar{x} = 8.6$). All other prey items were found in < 6.0% of the stomachs examined.

The distributions of stage-of-digestion values assigned to the food items in the stomachs of sharks caught by the two different fishing methods are shown in Figure 1. The distribution for sharks caught by rod and reel indicated that 71.8% of the food items were in either the first or last stage of digestion. In contrast, food items in the stomachs of sharks caught by gill nets were divided more evenly among all the stages of digestion. The two capture methods also differed in the proportion of sharks

TABLE 2.—Stomach contents found in a sample of 414 sandbar sharks.

Stomach content	No. of stomachs found in	Percent of stomachs found in
Blue crab, *Calinecties sapidus*	279	67.4
Empty	74	17.9
Atlantic menhaden, *Brevoortia tyrannus*	55	13.3
Summer flounder, *Paralichthys dentatus*	24	5.8
Unidentified fish	21	5.1
Mantis shrimp, *Squilla emprisa*	18	4.4
American eel, *Anguilla rostrata*	15	3.6
Spot, *Leiostomus xanthurus*	14	3.4
Atlantic silverside, *Menidia menidia*	9	2.2
Smooth dogfish, *Mustelus canis*	7	1.7
Northern pipefish, *Syngnathus fuscus*	6	1.5
Anchovy, *Anchoviella mitchilli*	5	1.2
Squid, *Loligo pealei*	5	1.2
Bluefish, *Pomatomus saltatrix*	3	0.7
Calico crab, *Ovalipes ocellatus*	1	0.2
Mummichog, *Fundulus heteroclitus*	1	0.2
Northern seahorse, *Hippocampus hudemius*	1	0.2

caught with empty stomachs. The percentage of the 178 sharks caught by rod and reel with empty stomachs (22.5%) was significantly higher than that found for the 236 sharks caught by gill nets (14.4%; z-test, $P = 0.015$).

Of the 414 stomachs examined, 203 contained a single food item. A stage-of-digestion value of 5 or 6 was assigned to 89 (43.8%) of these items, indicating that many sharks went at least the time equivalent of 5 stage-of-digestion units between meals (48 to 60 h for crustacean prey or 60 to 75 h for fish prey).

Multiple food items were found in 137 stomachs. The difference between the stage-of-digestion values

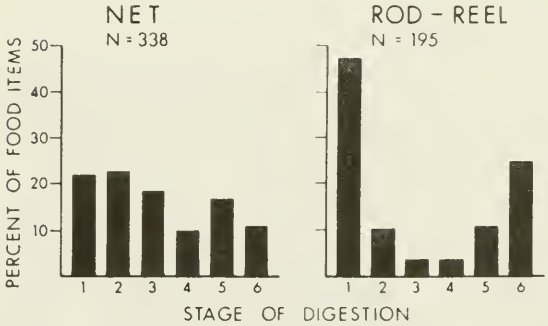

FIGURE 1.—Distributions of stage-of-digestion values assigned to food items present in the stomachs of sharks caught with gill net and rod and reel.

of the first and last eaten food items within each stomach was calculated to assess the amount of time that passed during consumption of multiple item meals. In 19 stomachs a food item in the sixth stage of digestion and one in the first stage of digestion were found. In these cases a time equivalent of 5 stage-of-digestion units had passed between consumption of the two food items, and since a stomach containing an item in stage 6 of digestion would be relatively empty, the two food items were considered to represent two different meals. Excluding the above 19 stomachs from analysis, the mean difference between the stage-of-digestion values of the first and last eaten food items was calculated for stomachs containing from 2 to 5 items (Table 3). The overall mean difference was 0.60 stage-of-digestion units indicating that multiple food items in the stomachs were in similar stages of digestion.

The quantity of food in each stomach examined was measured on a wet weight and dry weight basis. Excluding empty stomachs from analysis, the total dry weight of food (TDW) was found to be linearly related to the total wet weight of food (TWW) in the stomachs (TDW = $-0.24 + (0.22)$ TWW; $n = 318$, $R^2 = 0.96$). Since the two measurements were highly correlated ($r = 0.98$) and wet weight measurements have frequently been used in similar food studies on other species, it seemed valid to express the food quantity results in this paper on a wet weight basis. Table 4 summarizes the descriptive statistics of the quantity of food in 414 stomachs examined. The mean total weight of food found in the stomachs of sharks caught by gill nets was significantly higher than that found for sharks caught by rod and reel (18.91 and 13.09 g respectively; z-test, $P = 0.003$). Similar results were obtained when food quantity was measured as a percentage of shark body weight (0.96 vs. 0.76%; z-test, $P = 0.043$). This result, in conjunction with the other differences between the two capture methods mentioned above, suggested that sharks caught by rod and reel may not have been representative of the entire population (see section on Discussion). Because the primary value of the stomach content data in this study will be in the estimation of food consumed by the population, the following results concerning the amount of food in the stomachs were based on sharks caught by gill nets since they were probably more representative of the entire population of young sandbar sharks in the study area. For sharks caught by gill nets, crustaceans accounted for nearly twice as much of the mean total wet weight of food in the stomachs than did fish. The mean wet weight of crustaceans in the 236 stomachs (12.37 g) was significantly higher than the mean of 6.53 g found for fish (z-test, $P < 0.001$). Similar results were obtained when food quantity was expressed as a percentage of shark body weight (0.65 vs. 0.31%; z-test, $P < 0.001$). The mean weights of the two food components in the stomachs

TABLE 3.—Number of stomachs for which the stage-of-digestion value of the first eaten food item minus the stage-of-digestion value of the last eaten food item was equal to the given difference. The data are broken down into groups based on the number of food items present in the stomachs. Stomachs that contained an item at stage 1 of digestion and an item at stage 6 of digestion are not included (see text).

No. of items in stomach	No. of stomachs with indicated difference between stage-of-digestion values of first and last food items eaten: Difference 0	1	2	3	4	*N*	Mean difference	SD
2	44	25	9	0	1	79	0.60	0.78
3	13	17	0	0	0	30	0.57	0.50
4	2	3	2	0	0	7	1.00	0.76
5	2	0	0	0	0	2	0	0
Overall	61	45	11	0	1	118	0.60	0.78

TABLE 4.—Summary statistics of the amount of food in the stomachs of a sample of 414 sandbar sharks. Sharks were captured with gill nets and rod and reel gear. The z-test statistic was used to test the equality of the indicated pairs of mean values.

Stomach contents	Capture method	Mean	*N*	SE mean	Max	Min	z-test stat.	P-value 2-tailed test
Fish (g)	Gill net	6.53	236	1.10	114.80	0	3.74	< 0.001
Crustacea (g)	Gill net	12.37	236	1.11	102.20	0		
Fish (% BW)	Gill net	0.31	236	0.04	3.93	0	4.84	< 0.001
Crustacea (% BW)	Gill net	0.65	236	0.06	5.28	0		
Total (g)	Gill net	18.91	236	1.53	135.68	0	2.95	0.003
Total (g)	Rod and reel	13.09	178	1.25	100.30	0		
Total (% BW)	Gill net	0.96	236	0.06	5.28	0	2.02	0.043
Total (% BW)	Rod and reel	0.76	178	0.07	6.92	0		

were also calculated for each of eight consecutive 3-h time intervals of the day (Fig. 2). The means ranged from 1.05 to 14.92 g for fish, from 7.51 to 19.72 g for crustaceans, and from 11.74 to 34.64 g for the total wet weight of food in the stomachs. When 95% confidence bounds were placed around the means, considerable overlap of the confidence intervals was observed (Fig. 2). However, the mean total wet weight in the stomachs of sharks captured between the time of 0130 and 0430 was considerably higher than the other means, and the confidence interval for the mean during this time period overlapped substantially with only two of the remaining seven intervals. Similar results were obtained when food quantity was expressed as a percentage of shark body weight.

During the study one stomach was examined that contained a total wet weight of 444.0 g of food (10.3% BW (body weight)). This shark was not included in the results presented above because the quantity of food in the stomach was substantially greater than for any other shark. It is mentioned here because it does indicate that the stomach capacity of this species is considerably greater than the amount of food typically found in the stomach. In an attempt to estimate maximum capacity, the stomachs of 23 sharks were removed, ligated, and filled with water to the point at which they were about to burst. This point was determined by filling several stomachs until they burst and noting the changes that occurred in the stomach wall just before the bursting point. The average maximum capacity of the stomachs was found to be 13.0% of BW (range: 8.04 to 19.8%). For sharks caught by gill nets the mean quantity of food in the stomachs (0.96% BW) was 7.4% of maximum capacity and the largest quantity of food in a stomach (5.28% BW) was 40.6% of maximum capacity.

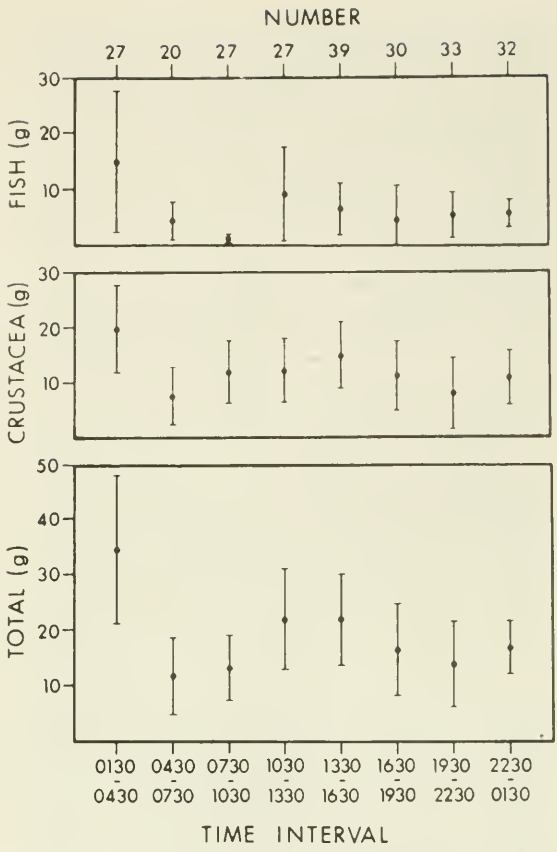

FIGURE 2.—Amount of food in the stomachs of sandbar sharks caught by gill nets during various time intervals of the day. Dots indicate mean wet weight in grams, and bars represent 2 standard errors on each side of the mean. The number of stomachs examined during each interval is given at the top of the figure.

DISCUSSION

Several investigations conducted in other areas have reported the sandbar sharks' diet to consist of small crustaceans and fish (Bigelow and Schroeder 1948; Springer 1960; Clark and von Schmidt 1965; Bass et al. 1973; Lawler 1977). With the exception of squid in several stomachs, the prey items of the sandbar sharks captured in Chincoteague Bay, VA, were also found to be small crustaceans and fish (Table 2) and agree with those reported by Medved and Marshall (1981) for this species in Chincoteague Bay. The studies above provided little specific information concerning the frequency of occurrence, size, relative amounts, or physical state of the food items. In the present study, small blue crabs that had recently molted were, by far, the predominant food item in terms of both weight and numbers. Small menhaden were also found to comprise a significant portion of the food consumed, but other species appeared to be of minor importance in the diet of the sandbar shark in the study area.

The results of this study strongly suggest that the feeding behavior of sandbar sharks in the study area was characterized by relatively short periods of feeding activity separated by substantially longer periods of time during which stomach contents were digested and no additional feeding occurred. An indication that this species may go relatively long periods of time without feeding was the high percentage (21.5%) of sharks that had a single food item in their stomach that was in a late stage of digestion (stage 5 or 6). Based on the approximate duration of each

stage of digestion (12 or 15 h depending on prey type) these sharks apparently had gone at least 48 h without consuming additional food. Another 17.9% of the sharks captured had empty stomachs. None of these were found to have an everted stomach, indicating that regurgitation of food was not responsible for the high percentage of empty stomachs. Additionally, 98 sandbar sharks fed preweighed meals and released in an enclosure in the natural environment were not observed to regurgitate food when recaptured at a later time (Medved in press). Thus it appears that the sharks with empty stomachs had not consumed food for a period of time greater than the time required to evacuate the last meal (at least 72 h). Given the long duration of gastric evacuation, a shark feeding nearly continuously would have many food items at various stages of digestion in the stomach. Multiple food items were found in some stomachs, but 90.6% of the stomachs contained less than three food items. Multiple food items in a stomach were also generally in similar stages of digestion (Table 3). The sharks with a single food item in their stomach consumed that meal in a very short period of time. The mean difference between the stage-of-digestion values of the first and last prey item consumed by sharks with multiple items in their stomach was 0.60 units (Table 3). Considering that digestion was divided into six stages, the feeding duration of sharks that consumed a meal of multiple food items was also very short relative to the time required for complete gastric evacuation. Observations made during a study of gastric evacuation in the sandbar shark also suggested that feeding ceased after the consumption of a meal (Medved in press). In that study the stomachs of 98 sharks were lavaged to remove all food and a preweighed meal was then fed to each animal. The sharks were released in a large enclosure in the natural environment that contained an abundance of prey and were recaptured at various times after feeding. Of the 54 sharks sacrificed within 40 h of feeding, only 4 had consumed additional food. In contrast, of 11 sharks that had their stomachs lavaged but were not fed a meal before release all but 2 were found to have food in their stomachs when sacrificed 24 h later. The results discussed above indicate that the feeding activity of sandbar sharks in the study area was intermittent rather than continuous. Similar models have been proposed in several other feeding behavior studies on fishes. Diana (1979) proposed an intermittent feeding model for the northern pike, *Esox lucius*, and suggested that such a model was appropriate for many top carnivores. Longval et al. (1982) have shown that after captive lemon sharks, *Negaprion brevirostris*, have fed to satiation, it takes a few days for the appetite to become reestablished. Carey et al. (1982) suggested that the great white shark, *Carcharodon carcharias*, may maintain itself for more than a month on a single large meal. Holden (1966) and Jones and Geen (1977) indicated that the spiny dogfish, *Squalus acanthias*, consumes a meal and then ceases to feed until digestion is complete. Observations made by Sano (1959) suggest that this may be typical of other shark species as well.

The differences observed between the stomach contents of sharks caught by the two capture methods are consistent with the model of feeding postulated above. The majority of sharks caught by rod and reel had stomachs that were empty or that contained food items in the first or last stage of digestion (Fig. 1). The sharks with empty stomachs had apparently not consumed food for a long period of time. Those with a food item in the last stage of digestion had relatively empty stomachs and had also gone a considerable time without feeding. Finally, the sharks with a food item in the first stage of digestion had eaten within several hours of being caught. Assuming that these sharks were actively feeding since they were inclined to consume the squid used as bait, it appears that the sharks in a "feeding mode" were those with relatively empty stomachs that had not fed for some time and those that had just eaten but were inclined to consume additional food. The stomachs of sharks caught by gill nets were empty or contained a single food item or multiple food items in similar stages of digestion suggesting, as indicated above, that feeding was intermittent. However, the stage-of-digestion values of the food items in the stomachs were spread more evenly over the digestion scale than for sharks caught by rod and reel, indicating that these sharks were in various stages of the feeding cycle (Fig. 1). The higher percentage of empty stomachs and lower mean stomach content weight found for sharks caught by rod and reel than for those caught by gill nets also suggested that sharks caught by rod and reel were those in a "feeding mode" and that sharks caught by gill nets were probably more representative of the entire population.

For sharks caught by gill nets the mean quantity of food in the stomach was 0.96% of BW and the maximum quantity was 5.28% of BW (Table 4). Considering that the mean stomach content was based on sharks containing food in various stages of digestion, it probably is a significant underestimation of the average meal size of sharks in the area. In contrast, the maximum quantity of food found in a stomach is undoubtedly an overestimate and the

average meal size should be considered to have been somewhere between the two values. It would then appear that the average meal size of the sharks captured was substantially less than the estimated stomach capacity (13.0% BW). The mean stomach content weights found for various time intervals of the day in this study suggested that sandbar sharks contained more food in their stomachs between 0130 and 0430 than during other times of the day (Fig. 2). The evidence was not overwhelming but these results do agree with a study by Medved and Marshall (1981), indicating that night hours may be a period of increased feeding activity for the sandbar shark.

Although this paper has provided a quantitative description of the stomach contents of the sandbar shark, data concerning stomach contents alone are not sufficient for estimating food consumption. As pointed out by numerous researchers, the amount of food in a fish's stomach is a function of both the rate of ingestion and the rate of gastric evacuation (Eggers 1977; Thorpe 1977; Elliott and Persson 1978; Jobling 1981). However, when combined with detailed information concerning gastric evacuation, the results of this study will provide the basis for the construction of an appropriate model of food consumption for the sandbar shark.

ACKNOWLEDGMENTS

We would like to acknowledge the management and staff of the Wallops Island Marine Science Center for their cooperation. This study was supported by the Narragansett Laboratory of the National Marine Fisheries Service, the Montauk (New York) Captains' Association, the National Wildlife Federation, and the Society of the Sigma Xi. It constitutes a portion of a thesis submitted by the first author in partial fulfillment of the requirements for the degree of Ph.D. in oceanography at the Graduate School of Oceanography of the University of Rhode Island. Special thanks go to Ann Durbin and Howard Winn for reviewing the manuscript and to Jim Donovan, Jeremy Donovan, Brad Thompson, Herb Morgan, and Todd Stephens for assisting with the field work.

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THE SPAWNING CYCLE OF SOFT-SHELL CLAM, *MYA ARENARIA*, IN SAN FRANCISCO BAY

SHELLY E. ROSENBLUM AND THOMAS M. NIESEN[1]

ABSTRACT

Four populations *Mya arenaria* in San Francisco Bay were studied for 1 year to determine the spawning cycle. The spawning cycle was well synchronized among the four populations. Gametogenesis had commenced by late February and spawning occurred uninterrupted from April through summer. Cessation of spawning occurred from September to October. The protracted spawning period of *M. arenaria* populations in San Francisco Bay is probably related to the long period of moderate water temperatures (March-October) which occur there. Size at first reproduction was placed at a shell length of 25 mm. Sex ratios of *M. arenaria* > 25 mm in shell length did not differ significantly from 1:1. No evidence of hermaphroditism was observed.

The soft-shell clam, *Mya arenaria*, was once popular with clam diggers in San Francisco Bay. During the early 20th century, owners of bay front property fenced off portions of the mud flats in order to exclude clam predators, thus insuring bountiful harvests of *M. arenaria* (Bonnot 1932). Today as the "trend toward the improvement of San Francisco Bay water continues,"[2] the potential for a recreational shellfishery exists again. Agencies for communities on the bay have begun to look at this potential. Recently (1982), the digging of clams in San Francisco Bay received official clearance for the first time in 30 yr.[3]

The spawning cycle of the soft-shell clam has been studied extensively on the east coast. Ropes and Stickney (1965) examined populations from the Cape Cod-New England region. They did not encounter clams in the ripe stage of gametogenesis until May, and by September spawning was over. Brousseau (1978) reported a biannual cycle of spawning for *M. arenaria* from Cape Ann, MA. The first spawning occurred between March and April and was of short duration. A separate, second spawning took place from June through July. Porter (1974) studied *M. arenaria* from populations at Skagit Bay, WA. He noted a single yearly spawning from late May to early September.

The climate of the San Francisco Bay area, and hence the seasonal water temperature fluctuations of San Francisco Bay, are much less extreme than that of the New England or Washington areas and most of the other locations from which *M. arenaria* has been examined. The question investigated in this study is whether the spawning cycle of *M. arenaria* from San Francisco Bay would differ from that of other areas reported in the literature.

MATERIALS AND METHODS

Description of Study Sites

Specimens of *M. arenaria* were collected from September 1979 through December 1980 from four sites around central San Francisco Bay (Fig. 1): 1) Candlestick Point–adjacent to the causeway leading to the Candlestick Park Stadium (lat. 37°42′32″N, long. 122°23′28″W); 2) Burlingame Lagoon–just south of San Francisco International Airport (lat. 37°35′12″N, long. 122°20′10″W); 3) Foster City–immediately north of the San Mateo Bridge, off Third Street (lat. 37°34′20″N, long. 122°23′28″W); 4) Point Isabel–north of the Golden Gate Fields race track on the eastern shore of San Francisco Bay (lat. 37°53′59″N, long. 122°23′28″W). These areas were selected because they experience annual variations in temperature and salinity (Conomos 1979), factors which are known to affect bivalve spawning cycles (Loosanoff and Davis 1951; Swan 1952; Matthiessen 1960, Pfitzenmeyer 1962; Stickney 1964). Substratum conditions were classified according to field observations; no particle size analyses were conducted.

[1]Department of Biological Sciences, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132.

[2]Jones and Stokes Associates, Inc. 1977. San Francisco Bay shellfish: an assessment of the potential for commercial and recreational harvesting. Prepared for the Association of Bay Area Governments, 171 p.

[3]Champion, D. 1982. Clam digging OK'd on part of San Francisco Bay. San Francisco, Chronicle, 27 August 1982, p. 1.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

The Candlestick Point site has a sandy substratum and is adjacent to a broad expanse of mud flat. Temperatures and salinities at this site reflect those of the central San Francisco Bay (Conomos 1979). Clams were collected high on the sandy beach front 0.6 m above Mean Lower Low Water (MLLW) in the areas exposed as the tide begins to recede.

Burlingame Lagoon is separated from San Francisco Bay by a levee with a narrow channel connecting to the open body of the Bay (Fig. 1). Salinity and temperature can vary dramatically with heavy rains (8 to 12 ppt) (pers. obs.). The area has a heavy clay-mud substratum. The collecting site was 0.6 m above MLLW.

The Foster City site was selected because it reflects conditions more closely associated with the south bay (Conomos 1979). The substratum is sandy-mud with rocks and cobble intermixed. The area juts into the bay and is exposed to wave action and temperatures and salinities characteristic of the bay waters (Conomos 1979). It is adjacent to outflow from the tidal channel that winds through Foster City. The collecting site was 0.24 m above MLLW.

The Point Isabel site is on the mud banks of a narrow (4 m wide) tidal channel that bisects the Point Isabel promontory. The substratum is clay-mud with rock and debris intermixed. Clams were collected from 0.15 to 0.46 m above MLLW.

The depths of the collection sites (relative to MLLW) at the four locations were dictated by the presence of *M. arenaria* at each site. *Mya arenaria* signals its presence by distinct siphon holes at the surface of the substratum. After an initial excavation of each collection site to a depth of 10 cm, it became obvious that clams were present only in the specific areas clearly marked by their siphon holes. Thereafter only these areas were sampled.

Temperature and salinity were recorded with a field hydrometer (marked at ppt) and thermometer at each site each month, beginning in October 1979 and continuing through November 1980.

Collecting Methods

A gardener's hand rake and careful hand digging was used for excavating the deep-dwelling *M. arenaria*. At least 25 clams were collected from each of the four sites each month for 1 yr (with the following exceptions: 4 October–Foster City, 12 collected; 3 November–Foster City, 20 collected; 25 December–Foster City, 24 collected; 2 November–Candlestick Point, 20 collected; 24 September–Point Isabel, 20 collected; 3 November–Burlingame, 7 collected). A total of 1,625 clams were examined in this study. Clams were collected, placed in a Thermos[4] jug of cool bay water, and returned to the laboratory.

Processing Methods

Analysis of gonadal stage was made by microscopical examination of histological preparations (Ropes and Stickney 1965). The presence and development of gametes was used to infer the spawning stage or readiness of the clam. Specimens were measured for shell length to the nearest 0.1 mm. The anterior one-third of the visceral mass (Ropes and Stickney 1965) was removed, labeled, and placed in Bouin's seawater fixative. During dissection, tissues were submerged in cool seawater to prevent drying or osmotic changes. The time between collection and preservation was under 3 h to prevent any gonadal changes.

The tissues were subjected to standard histological procedures (dehydrated in alcohol and embedded in paraffin). Embedded tissues were thin sectioned (5 μ) on a rotary microtome. Sections were mounted on glass slides, stained with Harris' hematoxylin and eosin, and examined using standard light microscopy.

Each slide of gonadal tissue was studied to determine the presence of male or female gametes and the condition of the gonadal tissues. This allowed clams to be placed into one of the five classes of spawning readiness (inactive, active, ripe, partially spawned, spent) employed and described by Ropes and Stickney (1965) for *M. arenaria*.

Categories of Spawning Readiness (adapted from Ropes and Stickney 1965)

Female Gonads

INACTIVE PHASE.–Ropes and Stickney (1965) used the term "inactive" to describe this phase. Brousseau (1978) preferred the term "indifferent" because cellular activity is continuing although no gametogenic activity is obvious. The term "inactive" is employed here and refers to individuals which are not seen to be producing gametes whether due to seasonal quiescence or immaturity. Thus in this research which presents pooled male and female data, the "inactive phase" may contain sexually undifferentiated individuals along with inactive animals clearly recognizable as male and female.

Females in the inactive phase exhibit small oocytes

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

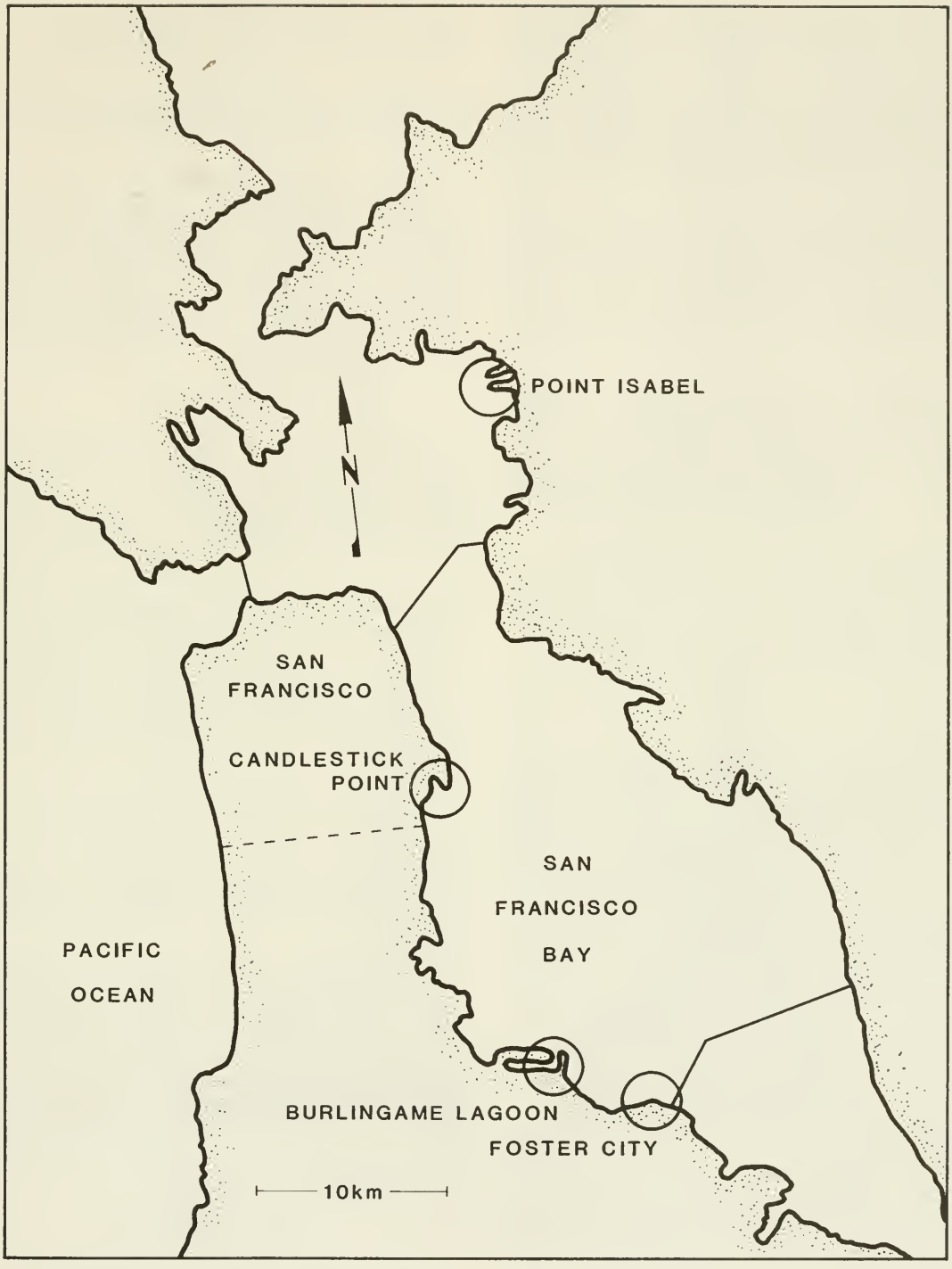

FIGURE 1.—Study sites on San Francisco Bay indicated by circles.

at the periphery of alveoli. Follicle cells completely imbed the oocytes and may fill the lumina of alveoli.

ACTIVE PHASE.–Enlarging oocytes grow between follicle cells towards the center of alveoli. Oocytes are irregular in shape but are attached to the wall of the alveolus by broad cytoplasmic bases.

RIPE PHASE.–In the ripe phase, oocytes appear as round cells in the lumina of the alveoli as if free of attachment to the basal membrane, yet they may be attached by a very slender stalk. The large oocytes fill the lumina of the alveoli and are usually more numerous than less developed oocytes.

PARTIALLY SPAWNED PHASE.–Gonadal tissues contain a few ripe oocytes. Small oocytes are imbedded in follicle cells at the periphery of an empty alveolus. Many alveoli are devoid of ripe oocytes.

SPENT PHASE.–Very few ripe oocytes are present, usually darkly staining with obscure nuclei. Numerous spherical droplets of lipoids and other products of cytolysis are characteristic. The spent phase progresses into the inactive phase.

Male Gonads

INACTIVE PHASE.–During the inactive phase, male tissues contain products of atypical spermatogenesis (Coe and Turner 1938). Tissues appear quite active, yet this activity will not result in viable male gametes. Pycnotic cells and multinucleated cells appear in the follicles. A few spermatogonia and primary spermatocytes may be seen at the periphery of alveoli while aberrant cells can be seen throughout the alveoli. As indicated in the description of the inactive phase for female gonads, this phase category is expanded to include sexually undifferentiated individuals along with pooled male and female inactive phase animals.

ACTIVE PHASE.–Proliferating primary spermatocytes exist at the basal membrane of the alveoli. These are small and uniformly sized cells which are similar to the earliest oocytes. They can be seen growing between follicle cells, extending toward the centers of the alveoli. Early stages of meiosis occur at the periphery of the alveoli, while later spermatids occur at the alveolar centers where they later form a distinct mass. Follicle cells eventually disappear.

RIPE PHASE.–Masses of spermatozoa arranged in more or less radial columns exist in rounded alveoli with tails oriented toward the center.

PARTIALLY SPAWNED PHASE.–Relatively few spermatozoa can be seen. Follicle cells start to refill the alveoli. Some pycnotic cells occur.

SPENT PHASE.–Spent male tissues contain no or very few spermatozoa in the central alveolar area. Numerous follicle cells with multinucleated cells and pycnotic cells from atypical spermatogenic activities surround small groups of spermatozoa. Tissues lack cells in the active phase of spermatogenesis. The spent phase progresses into the inactive phase.

RESULTS

Of the 1,674 clams examined in this study, 1,361 were distinguishable as male or female; the remaining 313 were indistinguishable as to sex. The male: female ratio (670:691) did not vary significantly from a 1:1 sex ratio ($P = 0.25$; $\chi^2 = 0.294$). No hermaphrodites were found. The possibility of asynchrony between males and females was considered. Separate histograms were prepared for the male and female data. Upon visual inspection the histograms showed no clear pattern of asynchrony between the sexes. As no discernable asynchrony was apparent, further analysis was considered unnecessary. The data for both sexes were pooled and are reported here.

The clams sampled in this study ranged from 15 to 88 mm in shell length. Of the 28 clams < 25 mm sampled, only a single 15 mm female in the active stage could be distinguished, the remainder showing no gonadal activity of any kind, sex being indistinguishable.

No consistent relationship between spawning condition and size could be discerned for clams over 25 mm in length. Correlation coefficients between size and spawning condition were calculated and subjected to a *t*-test, but the results were inconclusive. Clams of all sizes occurred in the various spawning categories throughout the spawning season. Mean shell lengths varied from 44.9 to 61.6 mm among the four populations studied (Fig. 2).

Candlestick Point

Sampling began in September 1979 and it was apparent that spawning was ending at that time. While 15% of *M. arenaria* were still ripe, 65% were inactive and the remaining 20% partially spawned or spent (Fig. 3). By late November, 95% of the clams

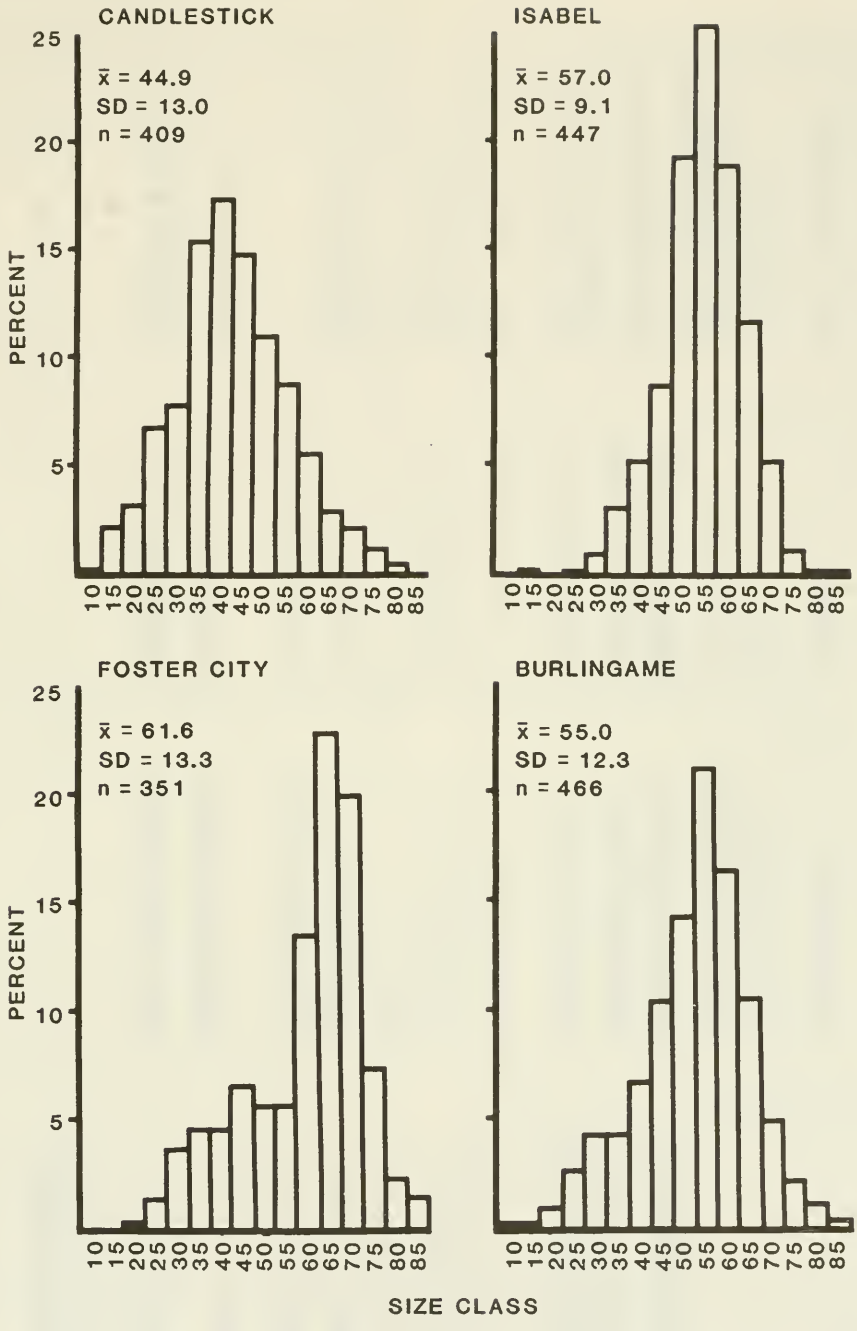

FIGURE 2. – Size-frequency histograms for the four populations studied. Size classes are (in mm) 10.0-14.9, 15.0-19.9, etc.

sampled were inactive and 5% still showed a few mature gametes which would probably have been resorbed. All individuals were inactive by the end of December 1979.

The first sign of gonadal activity appeared at the end of January 1980; by March, 82.1% of the clams sampled were active. In April, all individuals were either ripe or spawning. Peak spawning occurred

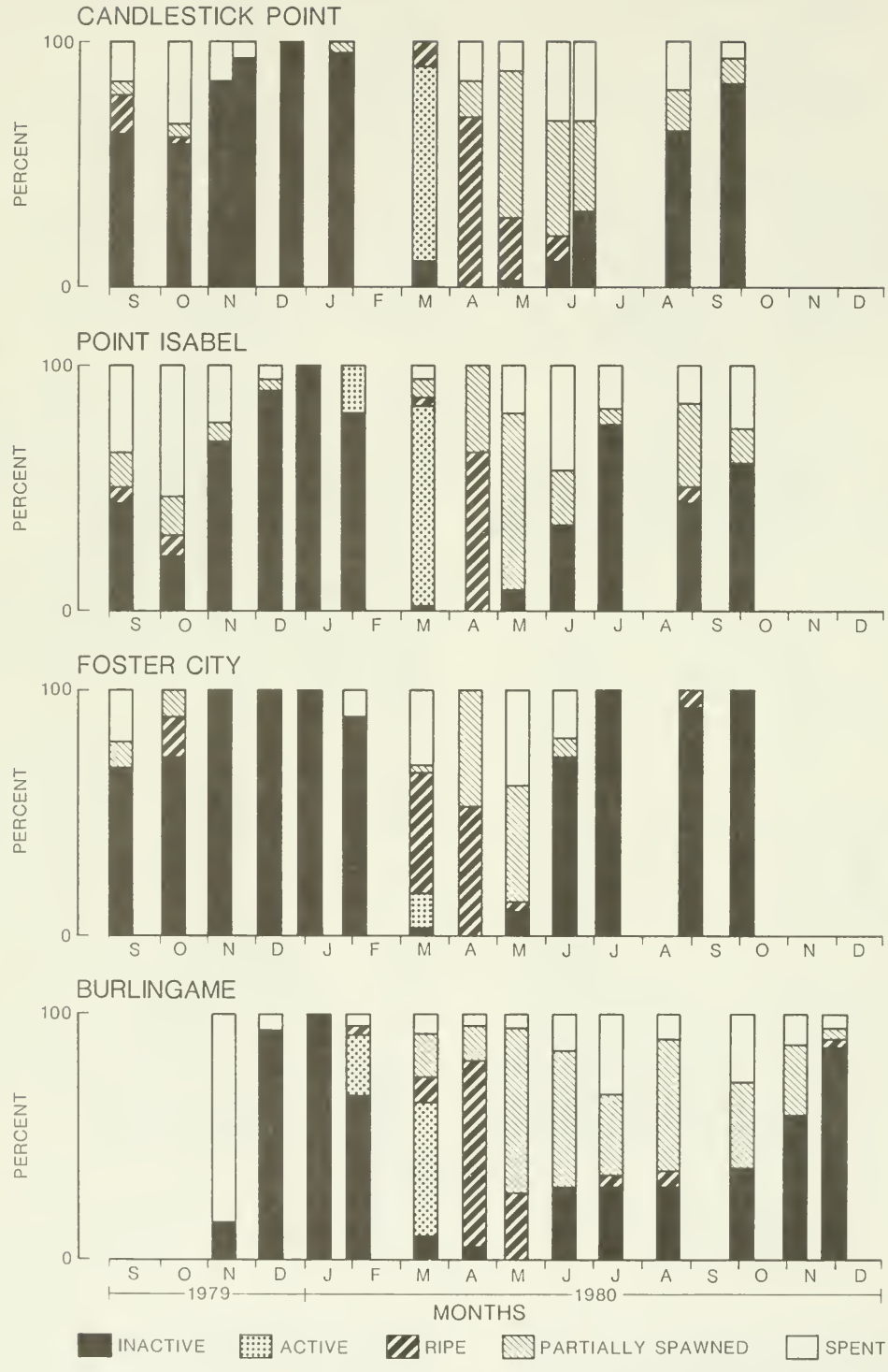

FIGURE 3.—Percentage of the clams sampled that were in each of the five categories of spawning readiness. Male and female data are pooled.

during May and June. By the end of June, the sample was roughly divided into thirds among the partially spawned, spent, and inactive stages. Some spawning could still be seen through the end of August, but by late September 85% were inactive, 10% partially spawned, and 5% spent.

Foster City

September-October 1979 marked the end of the Foster City population spawning, with most clams (70%) being inactive during this period (Fig. 3). From early November through the end of December 1979, no activity could be found. The late January 1980 sample showed a 90% active:10% spent ratio with no intermediate stages represented. It is unclear whether this indicated a rapid maturing and spawning of a few precocious individuals or an overwintering of residual gametes. By mid-March, every stage was represented, most (50%) being in the ripe stage. Peak spawning extended from the beginning of April through May, with a complete maturation-spawning season extending from late February through May. From July to late September no appreciable gonadal activity could be discerned. This lack of activity from mid- to late summer distinguished the Foster City population by its short spawning season relative to other populations (Fig. 3).

Burlingame Lagoon

Sampling of the Burlingame Lagoon population did not begin until November 1979. At the time 85% of the clams sampled were spent and only 15% were inactive (Fig. 3). This suggests a protracted spawning in 1979, similar to that which was seen in 1980. By December all but 5% were inactive and by 1 January 1980 all were inactive. Gonadal activity appeared again by the end of January 1980. Peak spawning occurred during May and June; however, spawning continued well into September and October with a full 30% of the clams of each sample being in the partially spawned stage. The Burlingame Lagoon population had the longest spawning season of the populations examined.

Point Isabel

Sampling of the Point Isabel population began in September 1979. The September and October samples still contained ripe individuals (< 10%), but most of the clams sampled were spent or inactive. By November, 70% of the clams sampled were inactive and by the end of December all were inactive (Fig. 3). The 1979 spawning season had ended for the Point Isabel population by early November.

Gonadal activity had resumed by late January. By March, 80% of the clams sampled were active. Only ripe and partially spawned individuals could be found in mid-April, and by May inactive individuals were being found (10%). Peak spawning occurred during May. Spawning continued through June and by July almost 80% were inactive and 20% partially spawned or spent. Spawning appeared to be over; however, the August sample contained almost 35% partially spawned and 5% ripe individuals. It is tempting to suggest a possible second spawning in August, but the May and June samples lacked active or ripe individuals, which suggest the August observation be attributed to sampling error. Spawning was still occurring in late September, as 15% were still in the partially spawned stage. At this time, however, 60% were inactive and 25% spent.

The four study sites showed similar trends (Fig. 4) in temperature and salinity. Temperatures fell from November through mid-January and rose from mid-January through the beginning of April and then stabilized. Temperature then climbed again from mid-May through July. The July-September temperatures were steadier at the Foster City and Burlingame sites than at Point Isabel or Candlestick Point, where they dropped markedly during this period. Salinity followed a similar trend, falling during the late winter months, and rising during spring and summer (Fig. 4). Salinity ranged from 8 to 33 ppt and temperature from 12° to 23°C.

DISCUSSION

The spawning cycle of *M. arenaria* in San Francisco Bay in 1980 was an extended one. Gametogenesis had begun by late January for three of the four populations sampled (Candlestick Point, Burlingame Lagoon, and Point Isabel), and by mid-March all five stages of gonadal development were represented in the Burlingame Lagoon, Point Isabel, and Foster City populations. Spawning had begun at all four sites by April; over 20% of the individuals from each sample were in the partially spawned or spent stages. The number of clams in these spawning stages reached a maximum during May and June 1980. Spawning continued through September and October and then ceased.

Only a single clam < 25 mm in length was found to have active gonads. This suggests that 25 mm might be generally recognized as the size at first reproduction for San Francisco Bay *M. arenaria*.

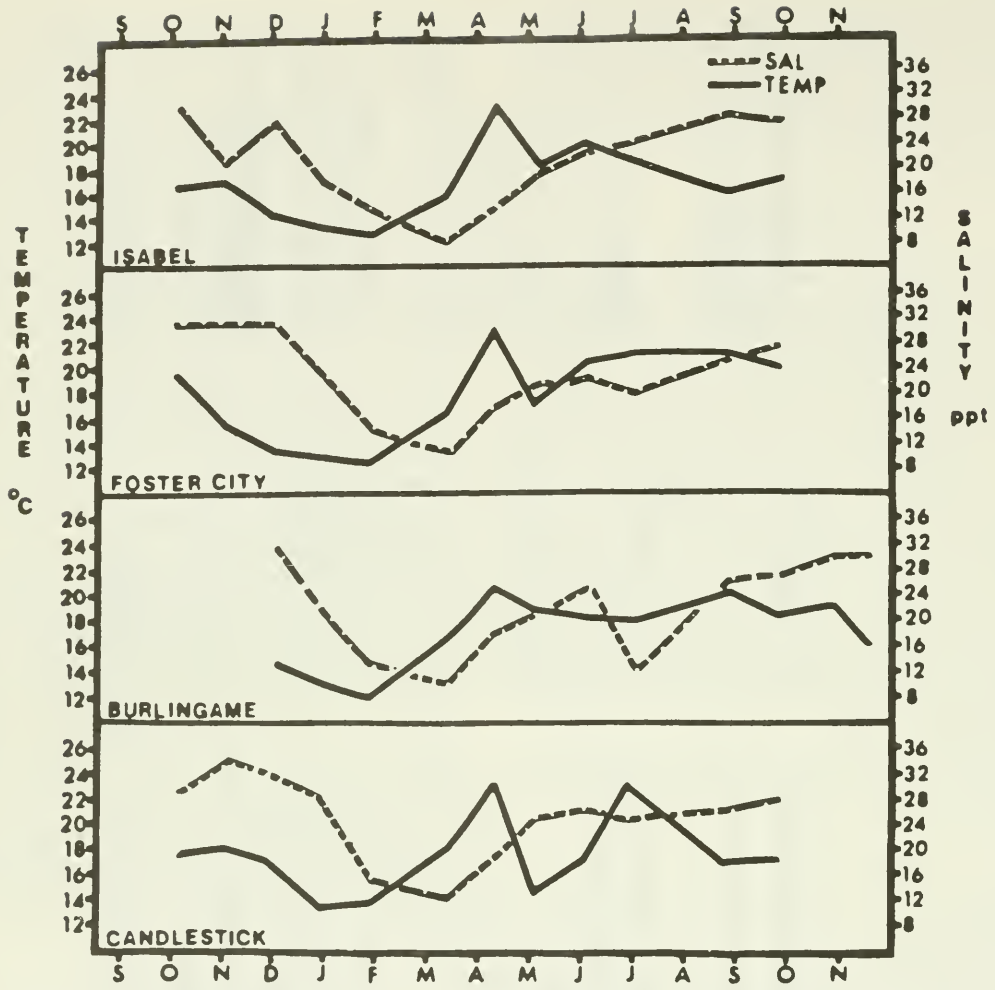

FIGURE 4.—Temperature and salinity variations during the collection period for the four collection sites, 1979 and 1980.

Although no growth or age measurements were performed in this study, the 25 mm shell length indicating a lower limit to sexual maturity corresponds to the east coast *M. arenaria* found to be late in their first year (Brousseau 1979).

Of the 313 clams that were indistinguishable as to sex, only 28 were < 25 mm in length, therefore we cannot attribute this lack of discernable sex to immaturity. Furthermore, clams of indeterminate sex were seen only during the fall and winter months (September-March) when most clams were found to be in the inactive stage. During the period of March-September or spring-fall when the active, ripe, partially spawned, and spent stages were well represented, all clams could easily be determined to be male or female. The difference between inactive male and female gonads is obvious and was seen in many clams, yet many clams which were larger than 25 mm in length and should have been sexually mature showed no signs of sexually distinguishable tissue at all. No evidence of even small oocytes or atypical spermatogenesis was seen in these clams. For the sake of simplicity, these clams were placed in the inactive stage. Perhaps this condition was a kind of "gonadal exhaustion" due to the prolonged spawning period.

The four study populations were dominated by clams ranging from 40 to 75 mm in length (Fig. 2). This size range corresponds to the 1.5 to 4.0 year classes determined by Brousseau (1979) for *M. arenaria* from Gloucester, MA. While total correspondence in growth rates between Massachusetts

and San Francisco Bay populations cannot be assumed, the age classes can be used as a first estimate of approximate age with size.

Studies of the spawning cycle of soft-shell clams from the east and west coasts of the United States reveal both similarities and differences in spawning pattern. Spawning on both coasts begins in early spring as the water warms from the lower winter temperatures. The majority of east coast populations studied show two separate spawnings each year, while populations studied on the west coast show a single more protracted spawning. Differences in the length of spawning and the number of separate spawning episodes are probably partially related to the phenology of water temperature change and the difference in the range of water temperatures that occur on either coast.

Mya arenaria in San Francisco Bay, studied during the 1979-80 season, began ripening earlier than *M. arenaria* of the New England region studied previously. Ropes and Stickney (1965) encountered active clams in eastern Maine by late January; however, ripe clams were not discovered until mid-May, and at that time none appeared to have spawned. Clams from their Booth Bay Harbor samples showed the earliest ripening, which was in April and May; by September spawning was over.

Brousseau (1978) reported a biannual cycle of spawning for *M. arenaria* from Cape Ann, MA. The first spawning at Cape Ann occurred as early as that in San Francisco Bay (March); however, it was of short duration, being over by April. A separate second spawning took place during June through July. Brousseau's figures indicate water temperatures began to rise from a low of 1°C around Cape Ann as early as mid-February, but did not rise above 10°C before May. It is possible that the increase in temperature triggered an early spawning, but the continuing, relatively cold temperature prevented an adequate build-up of mature gametes to sustain a prolonged spawning. Once spawning had taken place, the clams may have had to undergo another period of gametogenesis prior to a second spawning. Brousseau (1978, page 159) stated, "The presence of cytolyzed unspawned gametes in the summer samples suggested that the same individuals had also been ripe earlier in the year. Thus the observed spawning pattern was due to repeated spawning by the same individuals rather than asynchronous spawning of individuals within the population."

Pfitzenmeyer (1962) also reported two annual periods of spawning in *M. arenaria* at Solomons, MD. He noted that "The first umbone larvae of the year usually were found in May after the surface waters rise above 15°C or a mean temperature of 16.7°C." Salinities which remained constant throughout the spring remained near 10 ppt. This corresponds to the March temperature-salinity patterns in San Francisco Bay. During March, San Francisco clams were just beginning to spawn. Pfitzenmeyer also noted the disappearance of larvae from the Maryland waters as the temperature rose above a mean of 21.4°C. The larvae did not reappear until temperatures had fallen below this point. He concluded an optimal temperature range exists during which spawning may occur. In San Francisco Bay, temperatures rose to or above 21°C only in the following instances: Foster City–11 April - 23°C, 2 July - 21°C, 25 August - 21°C; Candlestick Point–9 April - 23°C, 30 June - 23°C; Point Isabel–10 April - 23°C (Fig. 4).

Porter (1974) noted a single yearly spawning from late May to early September among *M. arenaria* from Skagit Bay, WA. This is a shorter spawning season than seen among San Francisco Bay *M. arenaria* and may be a result of lower temperatures (4.8°-15.7°C) encountered in Washington.

Simel[5] reported a single spawning from late March through April for soft-shell clams from Humboldt Bay, CA. Generally, this more northerly part of California has a cooler climate than the San Francisco Bay area. Simel indicated that the later stages of gametogenesis corresponded with a peak in the phytoplankton abundance.

Studies of the spawning cycles of *M. arenaria* from the east and west coasts of the United States suggests a pattern of spawning behavior. Spawning begins as the water temperature rises in the spring. Pfitzenmeyer's (1962) work suggests *M. arenaria*'s optimal spawning range falls between 15° and 21°C. Differences between the spawning cycle of *M. arenaria* from San Francisco Bay and that of *M. arenaria* from New England, Canada, Washington, and northern California may be explained as the logical result of the different seasonal warming patterns and extremes encountered in the different areas. San Francisco Bay does not cool to the same temperatures as the other areas and has a much longer period of moderate water temperatures, extending from late March through summer and into September and October. Consequently, *M. arenaria*'s spawning season is equally protracted in San Francisco Bay.

[5]N. Simel, Humboldt State University, Arcata, CA 94542, pers. commun. 1982.

ACKNOWLEDGMENTS

We thank James Sutton of the California Academy of Sciences for his assistance with the selection of our study sites.

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RECRUITMENT PATTERNS IN YOUNG FRENCH GRUNTS, *HAEMULON FLAVOLINEATUM* (FAMILY HAEMULIDAE), AT ST. CROIX, VIRGIN ISLANDS[1]

W. N. McFarland,[2] E. B. Brothers,[3] J. C. Ogden,[4] M. J. Shulman,[5]
E. L. Bermingham,[6] and N. M. Kotchian-Prentiss[7]

ABSTRACT

During 1979 and 1980 the settlement of postlarval grunts (mostly French grunts, *Haemulon flavolineatum*) from the plankton to inshore areas in Tague Bay, St. Croix, Virgin Islands, was monitored. Settlement occurred at all times of the year, but showed two distinct maxima during May-June and October-November. Summer settlement rates were approximately one-third the peak rates, whereas winter settlement rates were low but always present. A dominant, semilunar periodicity in the settlement of the postlarvae was clearly present, but smaller interspersed weekly peaks occurred. Calculation of the fertilization dates of recently settled postlarval grunts, derived from otolith ages, also established a dominant 15-day periodicity, but again interspersed with smaller weekly fertilization peaks. The phase of settlement and fertilization is most strongly associated with the quarter moons and/or intermediate daily excursions of the tides; the smaller weekly peaks are more closely associated with new and full moons. The pelagic existence of French grunts is about 15 days, suggesting that fertilizations that lead to successful recruitment to inshore areas precede settlement by 15 days. Two hypotheses – semilunar shifts in spawning versus a more constant daily rate of reproduction – are discussed as possible explanations of the dominant semilunar rhythm observed in the settlement patterns.

Community structure is primarily determined by predation, competition, environment, and patterns of reproduction and recruitment (Ricklefs 1979). In most marine fishes the larval stages are planktonic, a circumstance especially true for tropical reef fishes (Breder and Rosen 1966; Sale 1980; Thresher 1984). In general, larger reef species produce numerous but relatively small eggs, which at spawning are dispersed into the plankton; whereas smaller reef species produce fewer but larger demersal eggs, which are guarded until hatching when the larvae also "escape" into the offshore plankton community (Johannes 1978; Barlow 1981). The potential significance of this widespread reproductive strategy to affect coral reef fish assemblage structure is widely recognized (see Helfman 1978 and Sale 1980 for reviews). Most ecologists have assumed that planktonic larval fishes provide an extensive reservoir of potential recruits that settle to the reef whenever space becomes available (Sale 1977, 1978; Dale 1978; Smith 1978). Virtually all recent studies, however, emphasize that we know little of the ecology of larval fishes at sea and of their patterns of recruitment to benthic juvenile habitats (McFarland in press; McFarland and Ogden in press). Until more quantitative information on the early life history of a variety of species of reef fishes is available, models that "explain" fish community structure remain, at best, first approximations. Here we describe spatial and temporal patterns of recruitment in the French grunt, *Haemulon flavolineatum*, a dominant western Atlantic tropical reef species.

MATERIALS AND METHODS

Recently settled postlarval French grunts and white grunts, *H. plumieri*, standard length (SL) ca. 8.5 mm, are commonly observed in schools over grass beds or associating with coral clumps and gorgonians in Tague Bay, St. Croix, VI. Single individuals and larger aggregations associate with structure and/or intermix with schools of mysids (McFarland and Kotchian 1982). There is little difficulty in recognizing and counting these very small grunts in the field because they lack the body colora-

[1]Contribution No. 70 of the West Indies Laboratory.

[2]Section of Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, NY 14853.

[3]Section of Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, NY 14853; present address: 3 Sunset West, Ithaca, NY 14850.

[4]West Indies Laboratory, Fairleigh Dickinson University, Christiansted, St. Croix, VI 00820.

[5]Department of Zoology, University of Washington, Seattle, WA 98195.

[6]Department of Biology, University of Massachusetts, Boston, MA 02125.

[7]Department of Zoology, University of Maine, Orono, ME 04473.

Manuscript accepted October 1984.
FISHERY BULLETIN: VOL. 83, NO. 3, 1985.

tion patterns of slightly larger postlarvae (see table 1 in McFarland and Kotchian 1982). Postlarval grunts, however, cannot be identified by sight at the species level. We will refer to these smallest postlarvae as PL-1 grunts. These recently settled postlarvae are diurnal plankton feeders (McFarland 1980) as, presumably, is the preceding pelagic larval stage. Although the postlarvae show strong social tendencies to school during daytime, they are solitary at night (Helfman et al. 1982); the same pattern is found in older juveniles and adults (Ogden and Zieman 1977). The typical stereotyped twilight migrations of older juvenile and adult grunts (Hobson 1968; Ogden and Ehrlich 1977; McFarland et al. 1979), however, are not present, nor are the agonistic behaviors typical of all later stages (McFarland and Hillis 1982).

During collateral studies on the population dynamics of grunts, on agonistic behavior in juveniles (McFarland and Hillis 1982), and age determinations of grunts (Brothers and McFarland 1981), we noted that recently settled PL-1's appeared in pulses. To investigate this periodicity, an extensive area of bottom in Tague Bay and a series of shallower discrete reef sites were censused repeatedly for PL-1's. In addition, subsamples of PL-1's were collected throughout the census period for size and age determinations.

Tague Bay Census Measurements

Sixteen flagged iron stakes were set 10 m apart along the bottom of Tague Bay parallel to the bay's barrier reef at a depth of ca. 5m. The bottom was characterized by sandhills produced by the burrowing activity of thalassinid shrimps, with stands of the seagrasses *Thalassia testudinum*, *Syringodium filiforme*, and *Halodole wrightii* between the mounds. Censuses of the total number of postlarvae were made using scuba, recording the numbers of grunts encountered along a 5 m wide transect. The census included all postlarval grunts observed over an area of 800 m^2 of bay bottom. Because almost all juvenile grunts in the immediate vicinity were French grunts, we presume the census data mostly represent this species. Of 85 PL-1's collected on this site, all were identified as French grunts. The census began on 25 February 1979, and was continued at variable intervals through 31 August 1980. Although numbers of older grunts were also recorded, here we report only the numbers of the smaller and youngest postlarvae (mean SL = 8.5 mm). This census is hereafter referred to as the "sandhill" site.

Reef Census Measurements

A series of 20 individual sites in a shallow sandy area (1-3 m depth) along a 200 m stretch of the Tague Bay barrier backreef were monitored for postlarval settlement. The sites varied somewhat in size and structure, but were composed of small clumps of *Montastrea annularis* and/or *Porites porites*. Sixteen of the sites were in depths of 1 to 2 m; four were in 2 to 3 m depth. Reef areas varied from 0.1 to 8 m^2; vertical relief from 20 cm to 1.5 m. Daily censuses were obtained as often as possible from 25 April 1980 through 25 May 1981. The census schedule was intensified especially from 6 May through 27 December 1980 (172 censuses over 236 d). Counts on each site on each census day included the total numbers of PL-1's, older postlarvae, juvenile grunts (see McFarland and Kotchian 1982), damselfishes (all species lumped), and the common sea urchin, *Diadema antillarum*, within the spines of which the middle-sized juveniles often seek refuge (see Helfman et al. 1982). In this reef area, which is surrounded by coral sand and lacks seagrass beds, juvenile white grunts were never encountered, only French grunts. We conclude therefore that recruits were all French grunts.

Reproductive Activity and Aging of French Grunts

Spawning in grunts has not been observed or reported in the literature (Breder and Rosen 1966; Hobson 1968; Johannes 1978; Lobel 1978; our personal observations and field observations of P. Colin and of E. S. Hobson). An indirect method was used to provide information on whether grunts spawned in some periodic manner, as so many reef fishes do (Johannes 1978; Lobel 1978; Colin 1982).

The age of French grunts can be established in days, for example, by counting the number of microstructural growth increments laid down in the lapillus (Brothers and McFarland 1981). The method is especially useful for aging the younger life history stages (< 100 d). By ascertaining the actual age of an individual grunt in days, it becomes possible to establish the specific date on which it was spawned. The method requires a correction, however, because the first "daily" growth increment deposited in the otolith does not coincide with fertilization of the egg. Our best "estimate" for the age at formation of the first distinct increment in the otoliths of French grunts is the third day after fertilization (for details see Brothers and McFarland 1981; this revised estimate is based on laboratory-reared porkfish, the con-

familial *Anisotremus virginicus*, of known age, supplied by Martin Moe). Thus, to each "otolith age" (= total increments counted) 2 d were added to establish the "absolute" daily age of an individual fish.

This method was applied to postlarval French grunts, collected throughout the year in the vicinity of the 20 discrete census sites. On most census days individual PL-1's were collected with a fine mesh net and fixed and preserved in 95% ethanol. Each postlarva was measured (SL) and the otoliths were removed and placed in immersion oil. The number of growth increments was counted and corrected (+ 2 d) to the actual date of fertilization.

Tides

A tidal gauge (NOAA, Ocean Survey #9751224) operates at the West Indies Laboratory dock, about 0.5 km from our Tague Bay study site. Hourly tidal heights for the year 1980 were obtained from NOAA. Missing, due to malfunction of the gauge, are records from 26 June to 9 September 1980. These missing values were approximated from calculated tidal data for San Juan, Puerto Rico. The phase of the tides in Puerto Rico matched closely the tides at Tague Bay (comparisons of dates before and after the missing records), but the actual excursion of the tides was less at St. Croix than calculated for Puerto Rico.

RESULTS

Tague Bay Sandhill Study Site

During 1979, 27 censuses were executed during 300 possible days of sampling (25 February to 21 December). The mean interval between censuses was 11.2 d ± 6.6 (1 SD), the intervals ranging from 4 to 23 d. Five population peaks were recorded, with the number of PL-1's counted between peaks often declining to < 100 individuals. The 1979 census clearly indicated that settlement was represented by a series of pulses, but the sampling intervals were too long to resolve periodicities of much less than 1 mo. Therefore, in 1980 the sampling resolution was improved by increasing the number of censuses to 47 over a possible 325 sampling days (6 February to 26 December 1980); mean sampling interval was 7.0 d ± 7.7, the shortest interval being 1 d and the longest interval 49 d (i.e., the first interval). Eleven peaks, of which 8 are distinct, establish that the postlarvae settle in pulses, with the population numbers on the bay bottom often decreasing to 0 between pulses (Fig. 1). Although the pulses in population numbers

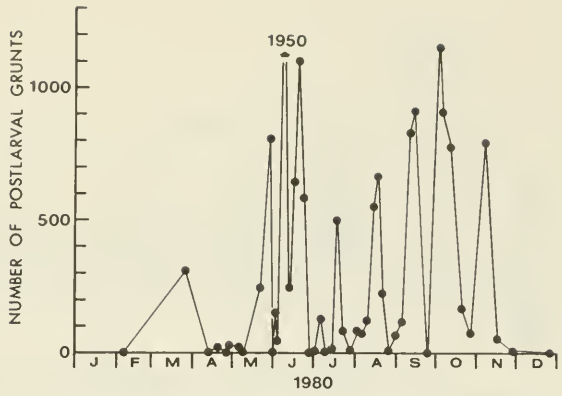

FIGURE 1.—Numbers of recently settled postlarval grunts observed over 800 m^2 of bottom on the sandhill site area of Tague Bay, St. Croix, V.I.

are suggestive of a semilunar periodicity, the peaks do not coincide more closely with either quarter moons or with the new and full moons than do the population declines.

Individual Barrier Reef Study Sites

The mean sampling interval on the 20 individual census sites from 6 May to 27 December 1980 (possible 236 sampling days) was 1.37 d ± 0.7 (1 SD). This shorter sampling interval vividly reveals the periodicity in the appearance of PL-1's on the sites (Fig. 2). Coincidence between these peaks and the peaks for the sandhill study sites is quite good (compare Figures 1 and 2) and indicates that the timing of the settlement of PL-1's is general over the entire area. Also, as in the sandhill area, the numbers of PL-1's declined to 0 between most pulses. Furthermore, the pooled data for the 20 sites indicate a bimodal seasonal influx of PL-1's, one in late spring and a second increase in fall, as seen also in the sandhill study site (compare Figures. 1 and 2). The summer settlement pulses involved about one-third the number of individuals associated with the bimodal peaks. Winter settlement was very low; only small numbers of PL-1's were observed during January and February 1981.

Age and Reproductive Activity

A total of 2,353 postlarvae from 141 collections spread over 391 d were captured between 20 February 1980 and 16 March 1981 (Fig. 3). From each of these 141 samples 15 PL-1's were measured and aged, or fewer if the collected samples contained

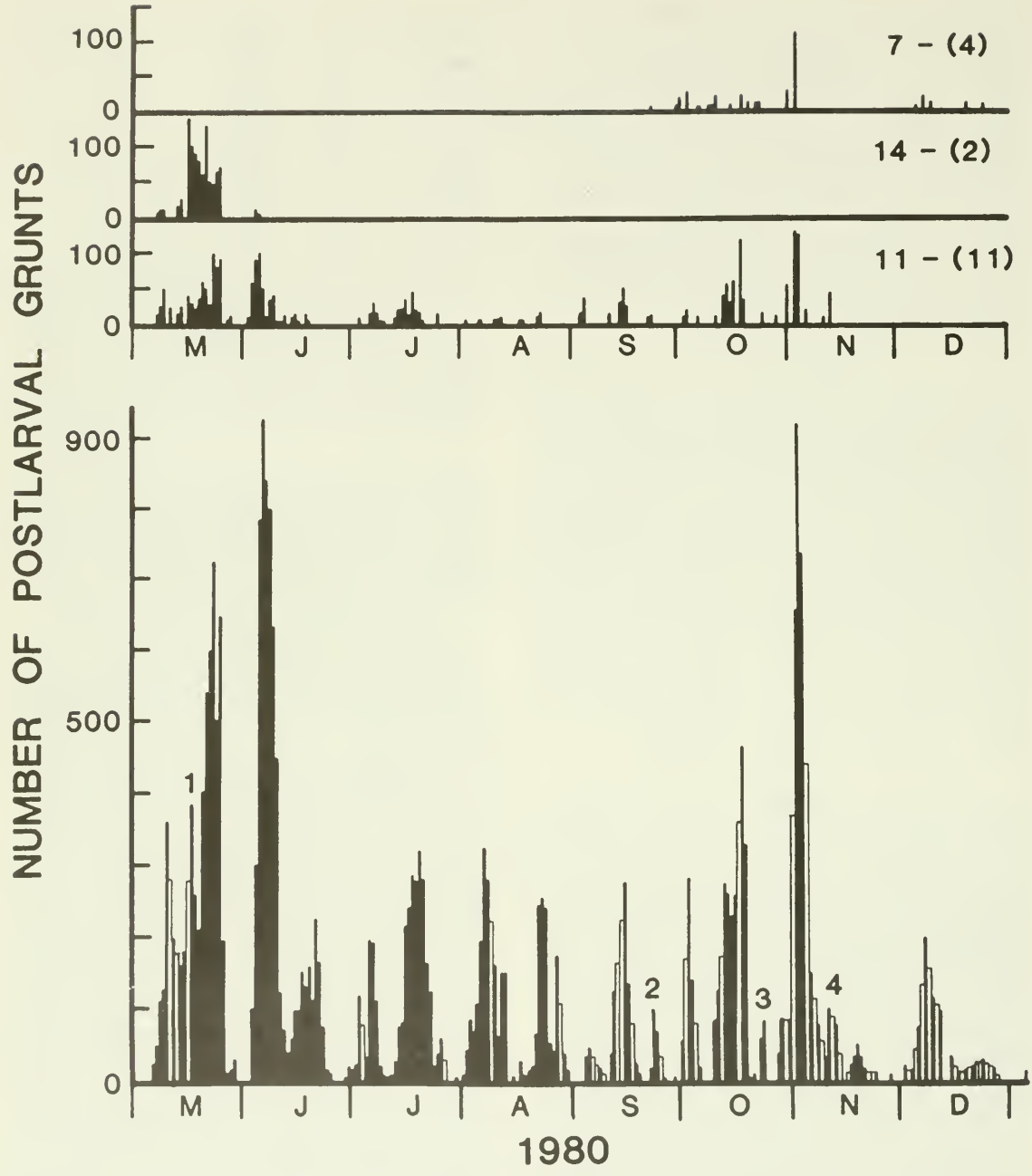

FIGURE 2.—Numbers of recently settled postlarval grunts observed on the individual census sites located in the shallows along the backreef of Tague Bay barrier reef. The three upper graphs represent the recruitment of PL-1's to specific sites 7, 11, and 14. Numbers in parentheses to the right of the hyphens indicate on how many sites a similar seasonal pattern of settlement was observed. Three of the 20 census sites were like 7 or 14, but also recruited grunts in summer (not shown). The lower graph represents the pooled data from all 20 sites. Values for census gaps have been estimated by calculating running averages (open bars). Numbers indicate the weaker but definitive weekly influxes of postlarvae. Additional weekly peaks probably occur but are less certain. Note the bimodal seasonal increase in recruitment during May-June and October-November: This coincides with the modal and bimodal peaks in gonadal development of several Caribbean reef species (Munro et al. 1973).

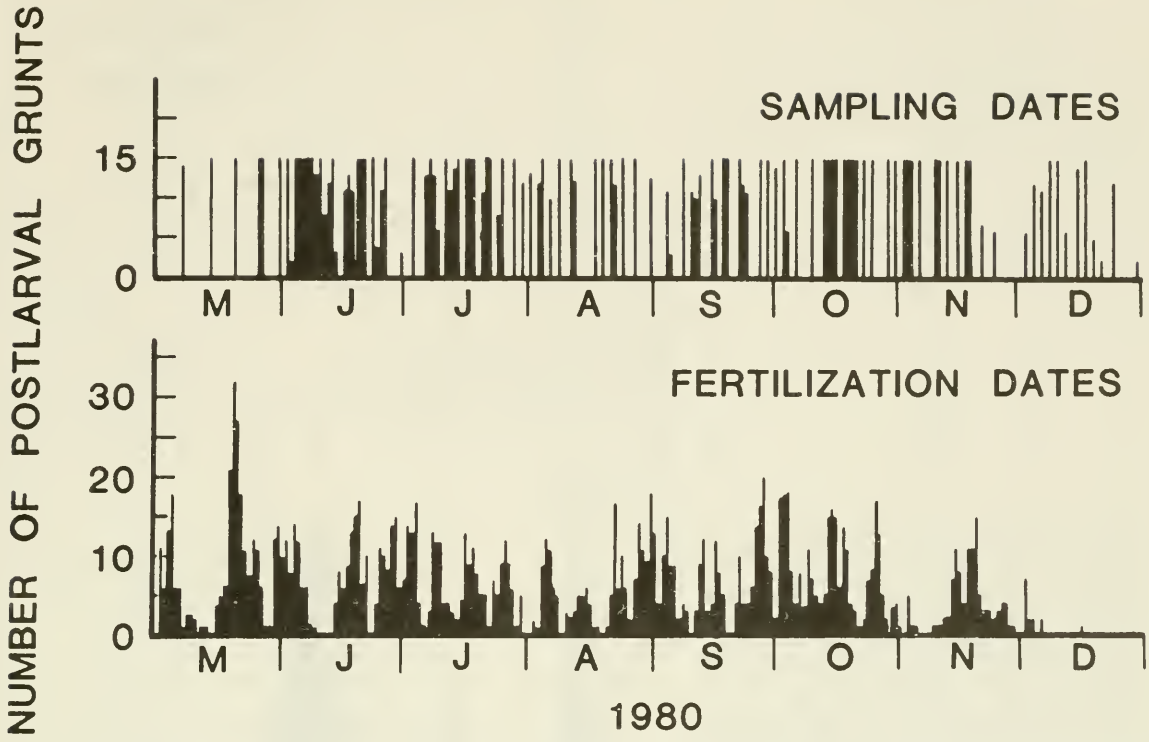

FIGURE 3. – Relationship of fertilization dates of recently settled postlarval grunts to time of the year. Upper graph represents the dates and the numbers of postlarvae collected for aging from the backreef of Tague Bay barrier reef. Lower graph represents the frequencies for back-calculated dates of fertilization of the collected samples in the upper graph.

fewer postlarvae (Fig. 3). The actual day of fertilization for each of these 1,478 French grunts indicates that recently settled individuals were spawned with a consistent periodicity (Fig. 3) that is similar to the settlement periodicity (Fig. 2). These derived spawning data suggest, however, the presence of a more pronounced short cycle.

Periodic Analysis, Times of Settlement and Reproductive Activity, and Patterns of Settlement

Periodic Analysis

To evaluate the periodicity of postlarval settlement and of fertilization times of recently recruited French grunts (Figs. 2, 3), we used a Rayleigh-test (see Batschelet 1965). The method involves a Fourier transform of sequential data (see McFarland and Kotchian 1982 for details). A data set is first sequentially summed for a specified period, and these pooled data are used to evaluate the degree of deviation from a nonperiodic random distribution. By comparing dimensions of the mean vectors obtained for different specified periods, the most dominant period is usually revealed (Fig. 4).

Analysis of the 1980 settlement and fertilization data reveals that a rhythm with a period of about 15 d dominates (Table 1). Examination of the census and fertilization data (Figs. 2, 3) indicates that weak secondary appearances of PL-1's and different fertilization dates may occur. Indeed, their presence (e.g., 4 peaks in Fig. 2) hints at a weekly rhythm superimposed on the semilunar periodicity. It is difficult to assess this possibility with periodic analysis, however, because a natural harmonic of the dominant 15-d rhythm can occur at about 7.5 d, even if a weekly rhythm does not exist (Fig. 4).

With less mathematical elegance the periodicity in the data sets can be estimated by averaging intervals between peaks. Both the 1980 census data for the 20 discrete study sites (Fig. 2) and the fertilization date data (Fig. 3) provide similar estimates of about 13.9 d and 15.1 d (Table 2), which do not differ significantly from the mean semilunar period of 14.64 d that actually occurred. The possible presence of a weekly rhythm often interspersed between the biweekly rhythm is revealed by 5 obvious short-period pulses

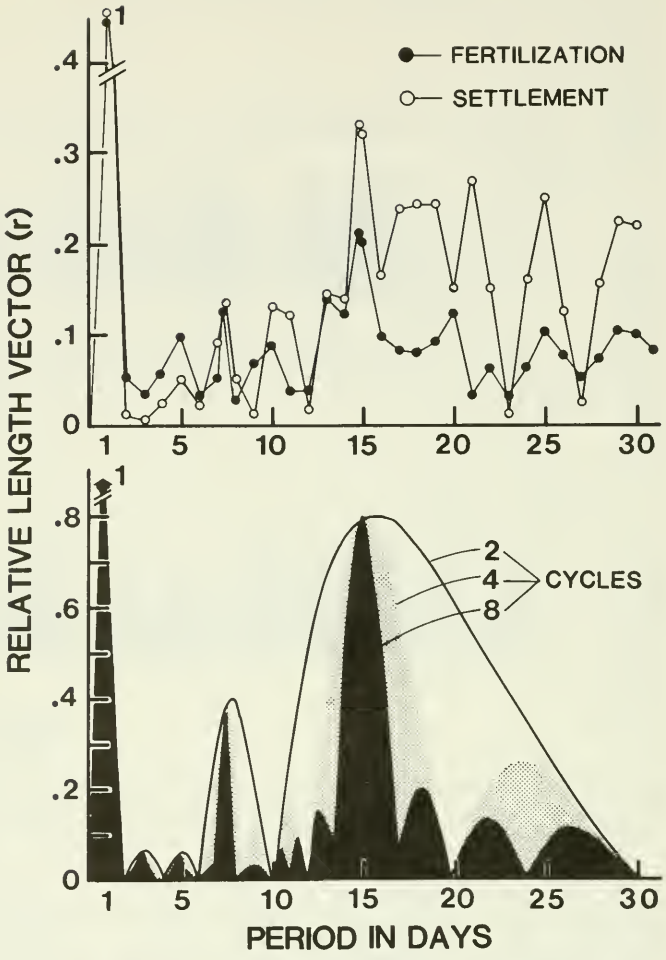

FIGURE 4.—Variation in the length of vectors derived from a circular distribution test for different periodicities in the settlement and fertilization data presented in Figures 2 and 3 (upper graph). Note that a period of about 15 d provides the largest vector value beyond a 1-d period (Rayleigh test statistic $z = 28.2$ for settlement and 10.8 for fertilization, where $z_{(P=0.01)} = 4.6$). Lower graph is a plot of vector values from artificial data generated by repeating the analysis for 2, 4, and 8 cycles (artificial data were 0, 0, 0, 0, 25, 50, 75, 100, 75, 50, 25, 0, 0, 0, 0). Note how an increased number of cycles or periods narrows the peak for the dominant 15-d period and introduces more harmonics. The settlement and fertilization data (upper graph) represent 16 cycles for a period of 15 d. The height of the harmonics after 15 d probably reflects basic sampling noise and the presence of smaller weekly peaks (see Figs. 2, 3).

TABLE 1.—Dominant periods derived from a circular distribution test of the settlement and fertilization data presented in Figures 2 and 3. Significance symbols are ** = $P <$ 0.01; z values are Rayleigh test statistic (Batschelet 1965).

Type of data	Date of samples	Dominant period (days)	z value	No. days	No. cycles analyzed based on dominant period
Settlement	30 Aug.-31 Dec.	14.9	26.5**	244	16.4
	2 May-31 Aug.	15.3	19.2**	122	8.0
	30 Aug.-31 Dec.	17.0	31.6**	124	7.3
Fertilization	2 May-31 Dec.	14.8	10.7**	244	16.5
	2 May-31 Aug.	14.6	8.7**	122	8.4
	30 Aug.-31 Dec.	15.5	2.8 n.s.	124	8.0

for settlement and at least 9 short-period pulses for fertilization (Table 2).

Timing of Settlement and Fertilization

To estimate the phase of settlement and of fertilization to the lunar cycle, the delay in days from the nearest full or new moon was determined for each event (Table 2). The mean phase delay for fertilization was 5.4 d, and for settlement 7.3 d. Clearly both fertilization and settlement are more often associated with the quarter moons than they are with the full or new moons. The overall relation to the lunar cycle is revealed more clearly by matching each in-

TABLE 2.—Comparisons of fertilization and settlement dates for recently recruited postlarval French grunts with the lunar cycle and the state of the tides. F and N are full and new moons; S and N are spring and neap tides; I↑ and I↓ are rising and falling tides of intermediate amplitude between a spring and a neap tide. The peak date for settlement represents the maximum influx of postlarvae, which occurred on average 3 d before the maximum number of French grunts appeared on a site. Values are the sums from all 20 census sites. Rows are aligned so that the most likely fertilization date precedes each settlement date. Vertical lines and summed numbers for days between peaks are best estimates of weekly peaks to yield the dominant biweekly peaks (see mean values at bottom of table).

Fertilization					Settlement				
Peak date	No. PL-1's in peak	No. days between peaks	Moon phase + days	Tidal state	Peak date	Total no. PL-1's in peak	No. days between peaks	Moon phase + days	Tidal state
—	—	—	—	—	4/7	[1]18	—	F + 7	I↓
—	—	—	—	—	4/22	[1]13	15	N + 8	I↓
—	—	—	—	—	5/7	360	15	F + 7	I↓
—	—	—	—	—	[2]5/14	383	7	N + 0	S
5/4	49	—	F + 4	S	5/20	723	6 13	N + 6	I↓
—	—	—	—	—	[2]5/26	29	6 13	N + 12	I↑
5/19	48	15	N + 5	I↓	6/3	930	7	F + 5	I↓
5/30	18	11	F + 1	S	6/18	224	15	N + 6	I↓
6/19	21	20	N + 7	I↓	7/3	195	15	F + 5	I↓
[2]6/28	20	9 14	F + 0	S	—	—	—	—	—
7/3	34	5	F + 5	I↓	7/17	317	14	N + 5	I↓
[2]7/7	21	4 14	F + 9	I↑	—	—	—	—	—
7/17	19	10	N + 5	I↓	8/4	324	18	F + 10	I↑
[2]7/25	16	8 19	F + 0	S	—	—	—	—	—
8/5	18	11	F + 11	I↑	8/20	255	16	N + 10	I↑
[2]8/10	8	5 15	N + 0	I↓	9/2	45	13	F + 9	I↑
8/20	12	10	N + 10	I↑	—	—	—	—	—
[2]8/30	24	10	F + 5	S	9/12	226	10	N + 3	N
9/3	15	4 13	F + 9	S	[2]9/20	100	8	N + 11	I↓
[2]9/12	17	9	N + 3	I↑	—	—	— 18	—	—
9/16	18	4	N + 7	I↑	9/30	280	10	F + 6	S
[2]9/21	11	5 15	N + 12	I↓	—	—	—	—	—
9/27	20	6	F + 3	I↑	—	—	—	—	—
[2]10/2	21	6 11	F + 8	I	10/15	462	15	N + 7	S
10/8	15	5	N + 0	I	[2]10/21	82	7 17	N + 13	N
[2]10/14	19	6 12	N + 6	S	10/31	917	10	F + 8	I
10/25	17	6	F + 2	I	[2]11/8	100	8 16	N + 1	I
[2]11/2	5	11	F + 10	N	11/16	50	8	N + 9	I
11/19	17	8 14	N + 12	N	12/5	199	19	F + 13	I
[2]11/25	5	6	N + 3	I	—	—	—	—	—
12/1	6	6	N + 6	N	—	—	—	—	—
Mean days between peaks									
including weekly peaks			7.6 ± 1.4 (2 SE)				11.5 ± 1.8 (2 SE)		
excluding weekly peaks			13.9 ± 1.6 (2 SE)				15.1 ± 1.1 (2 SE)		
Mean days from F or N moon			5.5 ± 1.5 (2 SE)				7.3 ± 1.5 (2 SE)		

[1]These two peaks are from sites adjacent to the 20 study sites and were abandoned after April.
[2]The peaks for these dates approximate weekly fertilization and recruitment pulses interspersed between the biweekly peaks for recruitment (see also Fig. 6).

dividual settlement date and fertilization date to the time of full moon (Fig. 5). Several features stand out: 1) The settlement data are less noisy than the fertilization data; this is explained, in part, by the more strongly expressed weekly patterns in the fertilization data. 2) Although settlement is clearly associated with the quarter moons, it does occur during other periods of the lunar cycle as well (see also Table 2, Fig. 2). 3) Fewer PL-1's are present on the sites during full moons than during new moons.

The relation of settlement pulses to daily tidal excursions (Fig. 6) indicates that settlement was most often associated with rising or falling (intermediate) stages of the tidal cycle than with spring or neap tides. A more extensive evaluation of the results reveals that out of 22 identifiable settlement pulses, 17 occurred during intermediate tides, 3 with spring highs, and 2 during neap tides. Also, out of 26 fertilization periods, 16 occurred during intermediate tides, 7 on spring highs, and 3 during a neap tide.

If a specific state of the moon, such as the quarter moons, is the significant environmental factor that determines the timing of fertilization and/or settlement of French grunts, then the state of the tides

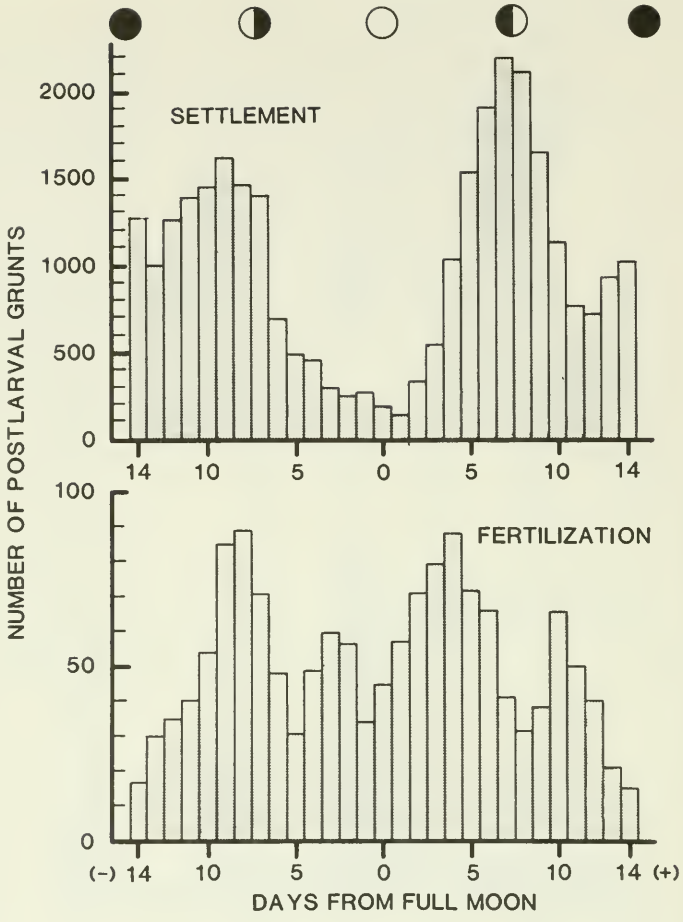

FIGURE 5.—Lunar phase relationships of settlement and fertilization dates for French grunts. Data represent the totals obtained from Figures 2 and 3 summed with reference to the days before and after full moons. The settlement data are the sum of peak numbers of PL-1's on all census sites. Actual settlement rates (maximum rate of influx) were maximal 2 to 3 d before the figured peaks. The fertilization data clearly reveal weaker weekly periods of spawning (see text for details).

should be unimportant. This condition would prevail because the tidal states (springs, neaps, intermediate conditions) change phase relative to the lunar cycle as the year progresses (Fig. 6). In contrast, if a particular state of the tide served as a primary trigger for fertilization and/or settlement then the moon's state would be unimportant. To test for the importance of tidal and lunar state the data were analyzed using a log likelihood statistic (g-test, Table 3) by grouping the 22 settlement and 26 fertilization peaks into the 9 possible combinations of tidal and lunar state (e.g., spring, neap, and intermediate tides and full, new, and quarter moons). Clearly both the lunar cycle and tidal state have significant effects on settlement and fertilization, but their interaction, although large, is nonsignificant. Because 60 to 80%

TABLE 3.—Summary of comparisons of lunar cycle and tidal state for fertilizations and settlement pulses of French grunts during 1980. Data from Table 2. Log likelihood test from Sokal and Rohlf (1981).

	g-value and associated chi-square					
Category	Settlement data			Fertilization data		
Total G[1]	36.7	$> \chi^2_{.001(8)}$	= 26.1	22.5	$> \chi^2_{.01(8)}$	= 20.1
Moon alone[2]	11.3	$> \chi^2_{.01(2)}$	= 9.9	7.3	$> \chi^2_{.05(2)}$	= 6.0
Tide alone[2]	18.0	$> \chi^2_{.001(2)}$	= 13.8	10.2	$> \chi^2_{.01(2)}$	= 9.9
Moon-tide[3]	7.4	ns $< \chi^2_{.05(4)}$	= 9.5	4.9	ns $< \chi^2_{.05(4)}$	= 9.5

[1]Single classification of all categories.
[2]Single classification of moon or tidal state alone.
[3]Two-way classification, moon phase versus tidal state.

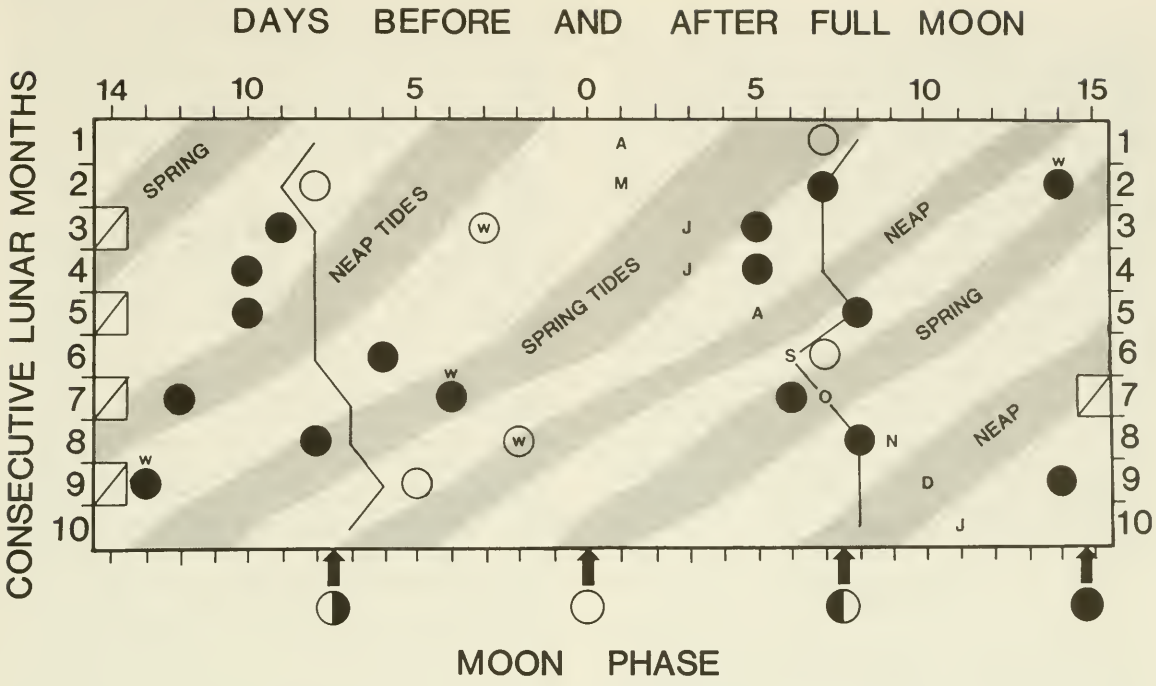

FIGURE 6.—Relation between the periodic settlement pulses of postlarval grunts during 1980, the phases of the moon, and the procession of spring and neap tides. Shaded areas represent relatively uniform series of neap or spring tides; unshaded areas are either increasing or decreasing intermediate tides (see Table 2). The sequence of days reads from left to right across each row. The first day of each calendar month is indicated by the letters, e.g., A at top = April 1980, . . ., J = January 1981. Closed circles represent the large and intermediate-sized pulses (> 100 PL-1's); open circles are settlement pulses with < 100 individuals (see Table 2). Closed and open circles with the letter w are weekly recruitment pulses interspersed between the more common biweekly peaks (see Table 2). The two abruptly changing vertical lines indicate the actual dates of the quarter moons at different times of the year, as determined from the Nautical Almanac for 1980. The mean deviations of those pulses most closely associated in each month with the quarter moons are: first quarter moon = 1.7 d ± 1.9 (SD), third quarter moon = 0.9 d ± 0.8 (SD). Maximum tidal excursions for spring tides occurred in May and June, and in October and November, as did the maximum recruitment of PL-1's to the census sites (Fig. 2, Table 2).

of the settlement pulses and fertilizations were associated with quarter moons and intermediate tides (Table 2), attempts were made to isolate the significant categories by combining the data (springs + neaps versus intermediate tides; full + new moons versus quarter moons). Nonsignificance occurred in all combinations with the exception of tides and settlement (g-test = 9.91 > $\chi^2_{.05(1)}$ = 3.84).

The relationship between fertilization and settlement of French grunts and the state of the tides and lunar cycle is obviously complex and difficult to unravel without ambiguity. Larger sample sizes (data over several years) would help, but perhaps more important would be specific data on current regimes at actual spawning sites and in the general vicinity of settlement sites. The highly significant but independent effects of moon and tidal state likely point at the importance of favorable currents to successful larval recruitment.

Settlement of Postlarvae in Space and Time

From May through December 1980, when the census frequency was high, there were 16 consecutive quarter-moon periods. On the 20 census sites, therefore, a total of 320 separate pulses (16 × 20) could have been observed if settlement did occur during the quarter moons. During this period 161 pulses were actually observed on the 20 sites during quarter moons. When the number of PL-1's settling was high, most sites recruited fish (90% for May-June, 75% for October-November). In winter, when the number of fish settling was low, recruitment nevertheless occurred on at least 4 or more sites during the quarter moons.

The periodic appearance of PL-1's on 11 of the 20 sites was virtually continuous at each quarter moon, and similar in general pattern to that depicted by the pooled data (e.g., site 11, Fig. 2). On 4 sites,

however, PL-1's settled in spring-summer or in summer-fall. These differences in the pattern of settlement between the census sites are highly significant ($P << 0.001$, "distribution-free" nonparametric test; Hollander and Wolfe 1973, p. 139-146). The patterns were so consistent, however, that we were soon able to predict with considerable success not only when, but which sites would attract PL-1's. We can provide no correlations with depth or area of a site, nor with the species of corals and other major residents (fishes, sea urchins, etc.), as to why some sites consistently "attracted" postlarval grunts and others varied, even though it is known that postlarval settlement can be partly governed by priority effects on reefs (Shulman et al. 1983). To understand the characteristics of a site that make it highly "attractive" to settling postlarval grunts will require sophisticated field manipulations.

DISCUSSION

The most conspicuous features concerning the recruitment of French grunts from the plankton are the rhythms in settlement and fertilization dates (Figs. 2-4). The continuing and short 15-d periods of these rhythms over an entire year contrast with other coral reef fishes where settlement, although rhythmic, is concentrated mostly around a particular period of the year (Williams and Sale 1981). Settlement in reef fishes is often episodic; it may show a lunar periodicity (Johannes 1978), it may be monthly but not coupled to a particular phase of the moon (Williams 1983 – mixed guild of pomacentrids), or a rhythm may not be conspicuous (Victor 1982, 1983 – *Thalassoma bifasciatum*).

The short period between fertilization and settlement implies that pelagic existence in French grunts is of short duration (about 2 wk; Brothers and McFarland 1981). To estimate the days spent in the plankton, the average age for the smallest 100 PL-1's was calculated from the sample of 1,478 fish that were used to estimate the actual day of fertilization [mean age = 15.7 d ± 2.1 (SD), range = 13-20; mean length (SL mm) = 6.9 ± 0.67 (SD), range = 5.9-8.5]. If each of these fish had settled from the plankton over the previous day, then pelagic existence (about 15 d) agrees with the periodicity of fertilization and settlement (Table 3, Fig. 4). In contrast, the pelagic existence of most other coral reef fishes investigated exceeds 15 d (Randall 1961; Johannes 1978; Sale 1980; Barlow 1981). This has been verified by results for age at settlement as determined from otoliths (Victor 1982, 1983; Brothers et al. 1983; Brothers and Thresher in press and unpublished; Thresher and Brothers in press). Most of these fishes settled at various ages: *Thalassoma bifasciatum*, 40-72 d; *Paragobiodon melanosoma*, 39-47 d; *Gobiodon* sp., 27-38 d; several unidentified scarids, 34-58 d; and labrids, 21-56 d. Direct aging of new recruits or otolith counts to presumed settlement marks rarely yield ages as low as found for the French grunt. Examples of species with pelagic phases of 20 d or less include the angel fish, *Holacanthus paru* (Brothers and Thresher in press); several damselfishes, *Glyphidodontops rollandi*, *Pomacentrus amboinensis*, *P. popei*, and *P. wardii*; the blenny *Petroscirtes mitratus*; the nemipterid *Scolopsis dubiosus* (Brothers et al. 1983); and the goby *Gobiosoma prochilos* (Brothers, unpubl. data). These may be exceptional cases; all or at least most of these species represent families characterized by having larval durations moderately to considerably longer than found in grunts. At the family level, therefore, only the haemulids, and perhaps the lutjanids, provide evidence of a short pelagic existence. In support of this conclusion is the lack of haemulids or lutjanids amongst the larval fishes collected offshore throughout the Caribbean (Richards 1981, footnote 8). Are haemulids programmed for short larval lives? We cannot be sure, but out of the 1,478 recently settled French grunts we have aged, not one exceeded 20 d from fertilization. Such a developmental process would be crucial in their survival; if they do not drift over suitable substrates on which to settle after 2 wk, they would perish offshore.

Our observations of a strong semilunar periodicity in French grunt recruitment, coupled with what seems to be a relatively fixed or invariant larval duration, could be the result of a number of different combinations of spawning and survivorship. Because we can only determine fertilization dates for individuals that have successfully recruited, we cannot be certain whether the apparent periodicity in spawning is an accurate representation of the temporal pattern of grunt reproduction. At the other extreme, it may be the result of relatively continuous spawning activity, the products of which survive differentially with respect to semilunar environmental variables.

Surprisingly, for such common fishes, little is known about spawning in haemulids. They produce pelagic eggs and larvae (Breder and Rosen 1966; Saksena and Richards 1975). Recently, paired spawning has been described for *Hapalogenys mucronatus* in aquaria (Suzuki et al. 1983). On six

[8]W. Richards, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149-1099, pers. commun. October 1980.

specific attempts to validate spawning in French grunts in the sea at St. Croix, two of us (McFarland and Shulman) failed to observe reproductive activity during dusk, but we did observe what appeared to be sporadic spawning by small groups of tomtate grunts, *Haemulon aurolineatum*, within large schools of these fish. These limited data suggest that grunts, like many reef fishes, cast pelagic eggs into the water column at dusk. We emphasize, however, that there are no data about their daily spawning habits.

Two hypotheses offer explanations for the dominant semilunar periodicity of fertilization and settlement.

Hypothesis 1. Assumption: Spawning follows a semilunar rhythm with breeding peaks closely coupled to the quarter moons (and/or intermediate monthly tides). If reproductive activities in French grunts follow a semilunar cycle, and pelagic life is programmed for 15 d, then settlement should occur most often during the quarter moons and intermediate monthly tides, which it does (see Table 3, Fig. 6). This hypothesis, however, does not account for the weekly peaks in settlement and fertilization (Table 3; Figs. 2, 3, 5), which contradict the assumption of the hypothesis.

Hypothesis 2. Assumption: Spawning is relatively constant from day to day, and larval existence restricted to about 15 d. Consistent daily reproductive effort could produce a continuous pool of grunts in the plankton. As a result, only those larvae that are favored by "correct" currents that disperse them inshore around 15 d will settle, and/or successful recruitment may also depend on favorable currents dispersing the eggs at the time of reproduction. At St. Croix we suspect that current conditions are most favorable to settlement during the quarter moons and intermediate tides. The weekly peaks that are associated with full and new moons (Table 3) could represent recruitment in less favorable currents than occur around the quarter moons. These currents, nevertheless, must allow some larvae through the "filter screens" that all recruits must pass through to join a reef community (Smith 1978). The semilunar rhythm of fertilization and settlement observed in settling grunts would, under this hypothesis, be explained by semilunar rhythms in currents favorable to settlement.

The time of day when settlement occurs and, especially, the amount of darkness at night may also relate to successful settlement. Although data are scarce, some reef fishes settle from the plankton at night (e.g., acanthurids–Randall 1961; McFarland, unpubl. data). We do not have similar direct observations for French grunts, but we suspect settlement is nocturnal because the number of PL-1's remained fairly constant on most census sites throughout each day. Nocturnal settlement behaviors would temporarily remove recruits from the attack of reef piscivores, especially if accomplished during the dark of the moon. During full moons, recruits presumably would be subject to higher rates of predation by planktivores than during other phases of the moon (Hobson et al. 1981). The number of grunts settling during full moons should be low, which it is (Fig. 4). In contrast, if length of darkness is a dominant factor to successful settlement, then the highest influx of recruits should coincide with the new moons, and intermediate numbers with quarter moons, which they do not (Fig. 4). The recruitment dynamics, nevertheless, indicate higher influxes of PL-1's when some degree of darkness occurs during each night (Fig. 4). We hypothesize that recruitment is dependent primarily on favorable currents, with predation possibly acting as a secondary selective force.

Reversals in surface currents and oppositely flowing currents in the upper 30 m, which could affect the dispersal of larvae, are known to occur at St. Croix and at Puerto Rico (Gladfelter et al. 1978; Lee et al. 1978; Molinari et al. 1980). Their local patterns, however, remain unknown. Eddy formation to the west of the island of Barbados, produced by Karmen trails as the generally west-setting current passes the island, has also been postulated to retain the pelagic stages of inshore species (Emery 1972). It is reasonably well established that seasonal shifts in local current gyres in the vicinity of Hawaii favor the settlement of various species of reef fishes (Sale 1970, 1980; Johannes 1978). In addition, spawning is often synchronized to disperse eggs and larvae away from reefs and into offshore currents (Johannes 1978; Lobel 1978). But specific currents do not always trigger spawning, as Colin (1982) reported for several reef fishes at Puerto Rico. In these instances, rhythmic spawning often can be related to the lunar cycle, but significantly, some species spawn every day. Depending on the time of spawning, dispersal routes for fish eggs and larvae can vary over short-time periods because of reversals in currents.

The daily behaviors and distributions of grunts at sea are unknown. Do larval grunts passively drift with currents? Or do they seek different depths at different times of the day? Active behaviors that would utilize differences in currents have been invoked to explain the retention of pelagic larval fishes and invertebrates close to the island of Oahu (Leis 1982). Similar activities by larval French grunts

could explain their absence in collections taken offshore (Richards 1981).

We have provided substantial evidence that French grunts recently recruited from the plankton are fertilized about 15 d earlier, and that these processes most closely correlate with the quarter moons and intermediate tidal excursions. Is this a general pattern that occurs throughout the Caribbean and western Atlantic where French grunts are most abundant? Or is the lunar-tidal correlation the result of local conditions? We have no answer at present, because it requires repeating the investigation in other localities. Different current regimes and local hydrographic conditions in other regions might elicit different recruitment patterns. The much weaker weekly fertilization and settlement patterns, for example, that are associated with full and new moons (Table 3) might dominate recruitment in other locales.

There is a seeming order in the rain of young French grunts from the plankton. Over the period of this study young grunts following a semilunar timetable appeared on over half of the census sites 70% of the time (range 59 to 94%). Although we could not discern any special characteristics of these sites that attracted grunts, the sites were never preoccupied by other species. Settlement certainly did not appear to be a random phenomenon. The recurrent order in the occupation of space by settling French grunts, however, may reflect only their high abundance in the reef communities at St. Croix (Gladfelter and Gladflelter 1978). Large populations produce large numbers of offspring and this alone might swamp available sites. In this regard we stress that the census settlement sites are not main reefs, but isolates adjacent to them. Indeed, large coral domes in the census area which sustained large populations of older juvenile French grunts never sustained populations of PL-1's. Without manipulative studies of grunts on the settlement sites, however, it is impossible to ascertain to what extent recruitment is influenced by a resident population (Shulman et al. 1983). We can conclude only that the recruitment of French grunts from the plankton has high temporal and spatial predictability at St. Croix.

Fishes in the family Haemulidae represent a dominant component of the tropical reef fish community and constitute a major part of the trap fishery in western Atlantic and Caribbean waters (Dammann 1980; McFarland 1980). The findings presented in this study provide insights that are critical to the management of any fishery for grunts. For example, the relatively short larval existence in French grunts, which also occurs in white and tomtate grunts (Brothers and McFarland 1981), implies that dispersal does not occur over very long distances. Whether local populations of grunts are self-sustaining or dependent on interisland transport is unknown. Answers will require precise knowledge of spawning habits of each species of grunt, careful analysis of local and general current regimes, and, if possible, the behavior of the larvae. If local populations are self-sustaining, then overly lenient limits on the harvest of adult grunts could seriously limit recruitment. In contrast, if recruitment shows large spring and fall peaks in other species of grunts, as it does in French grunts, and the seasonality in recruitment is geographically widespread (e.g. Munro et al. 1973), then closure of a grunt fishery for a few months during periods of peak recruitment would probably assure maintenance of the local populations.

ACKNOWLEDGMENTS

We thank Jack Sobel for his technical help in continuing the daily census routines when we could not be present, and Kim Benson who assisted in the otolith analysis. Numerous students at the West Indies Laboratory assisted as diving buddies; we thank them all. This project was supported by National Science Foundation Grant OCE-7918569.

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THE HARBOR PORPOISE, *PHOCOENA PHOCOENA*, IN FISH HARBOUR, NEW BRUNSWICK, CANADA: OCCUPANCY, DISTRIBUTION, AND MOVEMENTS

David E. Gaskin and Alan P. Watson[1]

ABSTRACT

The distribution, movements, and relative population abundance of harbor porpoises were studied in the Fish Harbour region of New Brunswick, Canada (lat. 44°59'30"-45°01'00"N, long. 66°54'00"-66°57'00"W), from 1970 to 1978. In any given year numbers of this species were highest in the region between late July and early September. This is also the period during which surface temperatures attain a maximum (10°-12°C) and the largest herring, *Clupea harengus*, catches are usually made. During July-September the porpoise population of the inner (western) part of the study area contained 63% mothers with calves. Changes in relative population abundance were most strongly related with time of year (increasing from early July), tidal amplitude (most present when amplitude is 6.5 m or less), and wind phase (most present during onshore winds). Observation of recognizable individuals revealed consistent specific "territories" and patrolling patterns. A marked decrease in relative abundance in the latter half of the 1970s was noted. This decrease was coincident with a decline in mean midsummer surface temperature over 1974-78 of about 1°C. Unfortunately it was not possible to determine from existing data if major changes in availability of prey species also occurred in the inner Quoddy region during the same period.

Literature concerning ecology of the harbor porpoise, *Phocoena phocoena*, has been largely restricted to reports of nonquantitative or casual observations (Scheffer and Slipp 1948; Møhl-Hansen 1954; Amundin and Amundin 1974), although more recently Gaskin (1977), Prescott et al. (1981),[2] Flaherty and Stark (1982),[3] Kraus et al. (1983),[4] and Taylor and Dawson (1984) have presented information from surveys and some population estimates for limited areas of both east and west coasts of North America. A population estimate for the Copper River area of Alaska was provided by Matkin and Fay (1980). Habitat indices, relating occurrence of animals in coastal waters to various environmental factors have been given by Smith and Gaskin (1983) and Watts and Gaskin (in press), and some radiotelemetric studies of distribution and movements by Gaskin et al. (1975) and Read and Gaskin (1983, in press).

In order to gain insight into the nature of local distributions and movements of *P. phocoena* over an extended period, we selected a semi-enclosed area of limited size in southern New Brunswick, Canada. Preliminary observations had already shown that the species was common in the area, and locality (about 8 km^2 maximum) bounded approximately by lat. 44°59'30"-45°59'00"N, long. 66°54'00"-66°57'00"W on the east coast of Deer Island (Fig. 1) was easily accessible for research and relatively sheltered. We were also aided by the occurrence in the area of several recognizable porpoises with surface disfigurements, large blemishes, or distinctive pigmentation patterns visible at some distance in favorable light; several of these animals were present in successive seasons.

CHARACTERISTICS OF THE STUDY AREA (Figure 1)

Average depths range from about 8 m in Lords Cove to about 22 m in Simpson's Passage (respective maxima 20 m and 60 m) at mean low water. The region is subject to anomalistic, semidiurnal tides of

[1]Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada.

[2]Prescott, J. H., S. D. Kraus, P. Fiorelli, D. E. Gaskin, G. J. D. Smith, and M. Brander. 1981. Harbor porpoise (*Phocoena phocoena*): Distribution, abundance, survey methodology and preliminary notes on habitat use and threats. Final report to U.S. Department of Commerce, NOAA, National Marine Fisheries Service Contract 80-FA-d-00009, 61 p.

[3]Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound". Final report for Subcontract 80-ABA-3584, NOAA, NMFS, National Marine Laboratory, Seattle, WA, 84 p.

[4]Kraus, S. D., J. H. Prescott, and G. S. Stone. 1983. Harbor porpoise, Phocoena phocoena, in the U.S. coastal waters of the Gulf of Maine. A survey to determine seasonal distribution and abundance. A report to the National Marine Fisheries Service, Woods Hole, Massachusetts, July 1983, 15 p.

Manuscript accepted October 1984.
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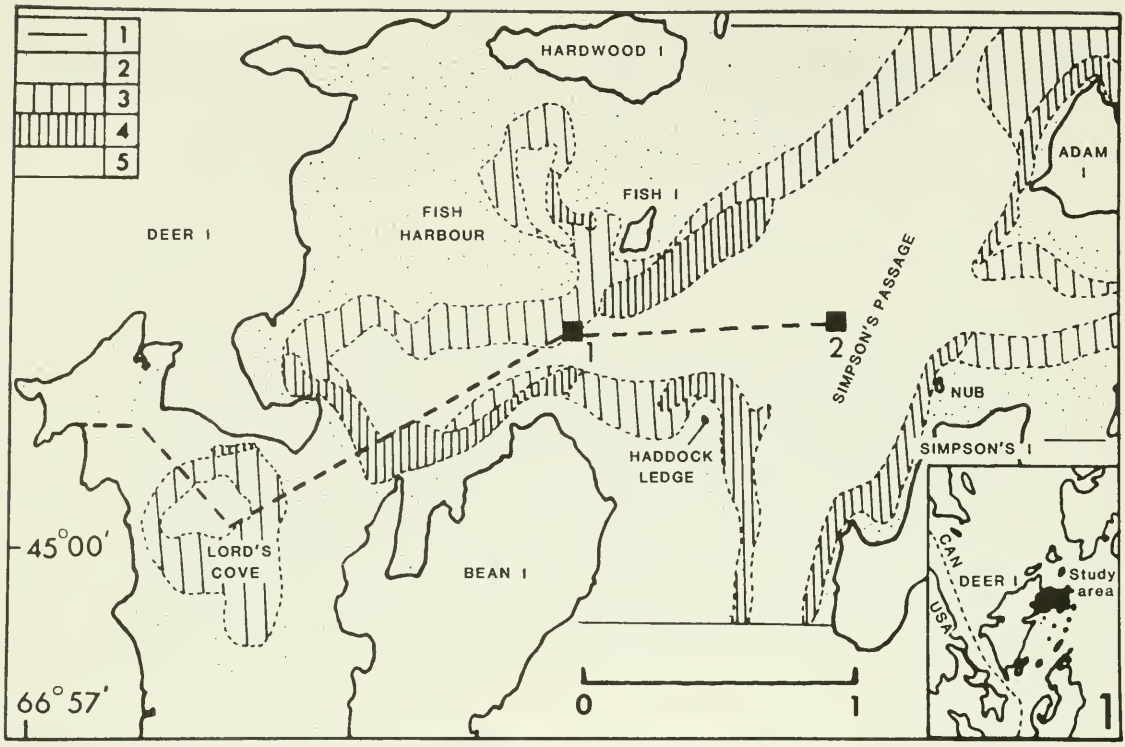

FIGURE 1. – The Fish Harbour region on the east coast of Deer Island region, New Brunswick, Canada (see inset). Legend: Straight solid lines indicate approximate limits of study area. Stipple indicates shallow shelf area (low water mark to 5 m); widely spaced vertical lines indicate areas of relatively gentle slope; narrowly spaced bars indicate steep scarps or slopes terminating in cliffs and the white areas (other than within island boundaries) are relatively deep basins and channels. Broken line shows regular track of boat with watch-stations 1 and 2. Place names are those used in the text. Scale = 1 km.

5.6-8.3 m (mean about 6.3 m) (Forrester 1960). Water turbidity is high (Secchi disk reading in July-August about 2 m). Most tidal flow from the area is by the northern end of Simpson's Passage. Salinities in the whole Quoddy region (Trites 1962) range from 29.5‰ (March-May) to 32.3‰ (September). Lower salinities in shallow inshore waters occur after heavy rain and may last for several days. While some year-to-year changes in mean surface temperature were recorded (Trites 1962, fig. 11), one of the most complete series (for 1978) provides a typical sequence of the relative changes from spring to autumn. Late May-early June surface temperatures ranged from 6.0° to 7.1°C, mid-July from 8.4° to 9.6°C, and mid-August-early September from 10° to 11.2°C. By early December the waters were 7°C again. Peak summer values of 11.3°-14.5°C were only obtained in mid-August at the head of Lords Cove in shallow water (< 5 m). At any given time surface temperatures were 0.5°-1.0°C warmer than those at 12 m despite the tidal mixing which obviously occurred. A general pattern of temperature profiles could be recognized in midsummer: The inner (western) part of Fish Harbour was vertically well-mixed throughout, but a rather steep horizontal gradient of about 1.0°C was maintained at all depths on the outer margin of this zone. In the central region (near Fish Island) the direction of water movement showed up to 90° variation at different depths at any given time of rapid tidal flow. The outer parts of Fish Harbour, and Simpson's Passage, tended to be well-mixed vertically, but were always about 0.5° cooler at the surface on the ebb. North of Adam Island there was a shift from horizonal gradients on flood to vertical gradients on the ebb. The inshore water is probably "trapped" in the bight of the harbor, i.e., with an extended residency time, while movement of water in and out the northern and southern entrances probably creates some mixing in the outer and central part of Fish Harbour. More detail of the static and dynamic characteristics of the study area and adjacent regions is provided by Smith et al. (1984).

METHODS

Most observations were made from a 5 m two-seater kayak (weather permitting), which appeared to exercise a negligible effect on the behavior of animals even at short distances (Watson 1976). A small fishing boat was used above Beaufort wind force 2, but this craft lacked the silent maneuverability of the kayak. Few publishable photographs were obtained because this species is an exceedingly difficult photographic subject. The method of making and maintaining contact was consistent throughout the study period (1 June 1970-10 September 1978). A central route from the head of Lords Cove was followed (Fig. 1); unless weather was too poor for optimal sighting in Simpson's Passage, or there was specific intent to track a group within Fish Harbour, the boat continued on track to watch-station 2 (Fig. 1). If no animals were present in Fish Harbour and conditions were less than Beaufort wind force 2, the boat would remain in the vicinity, but if the animals were already within Fish Harbour, the boat usually returned to watch-station 1 in outer Fish Harbour, from which point most of the study area normally used by porpoises could be kept under eye or binocular surveillance. As weather permitted, or presence and movements of animals dictated, this search pattern was usually repeated during the day at invervals of several hours. When porpoises were located either visually or from the sound of their expirations, the position of the boat and the initial positions of animals relative to the vessel were recorded to within a few tens of meters by taking 3-5 bearings from the many surrounding landmarks. Subsequent positions were noted in those cases when movements were tracked for extended periods, providing the animals surfaced long enough for accurate bearings to be taken and had moved to a significant distance (ca. 100 m) from the previous location. The time, location, size, and apparent composition of each porpoise group was recorded on and later transcribed from tape. The particular problems of quantifying sightings of this small cetacean have been considered by Gaskin (1977), Prescott et al. (footnote 2), Taylor and Dawson (1984), Kraus et al. (footnote 4, 1983), and Watts and Gaskin (in press). During the present study we used only data obtained in Beaufort Sea state 0-1, when visibility was unlimited within the study area and lighting was direct or diffuse, but uniform. In these ideal conditions some porpoises can be detected even from the air (250 m) at 650 m, although this is the least satisfactory method for sighting this species (Kraus et al. 1983). In a simultaneous comparison of effectiveness of stationary, mobile, and aerial observers (Kraus et al. 1983) the former, whether on land or stationary vessel, not only saw far more animals than the observers in the aircraft, but could detect them using binoculars in calm water at 1,000+ m. The probability of contact is enhanced when animals tend to surface repeatedly. The present authors found that porpoises working near the Nub close to the Simpsons Island (Fig. 1) could be clearly seen with binoculars from watch-station 1, at a distance of > 1 km in optimal conditions.

Some natural constraints on distribution of porpoises within the study area reduced the effective survey region to only 4 km^2. Virtually no animals ventured farther inshore than the shallow shelf edge (ca. 5 m) even during high water. Almost all ingress and egress was between Bean and Fish Islands (Fig. 1). Very few animals left by the southern passage from Lords Cove, and only two were ever noted to enter this way. Only one group of animals consistently visited Lords Cove in any case. No movement was noted through the narrow gut west of Hardwood Island, and only infrequent movement ($\leq$ 5%) through the passage north of Fish Island.

Harbor porpoises in the Quoddy region appeared generally indifferent to boat traffic (Watts and Gaskin in press), with no noticeable attraction bias as noted for *Phocoenoides dalli* by Kasuya and Jones (1984). Because of the small size of the study area, the impossibility of making random transects, the highly clumped distributions, and nonrandom movements of animals (see latter), any kind of line-transect approach was inappropriate. From a combination of the initial strip census search and the stationary observations, we concentrated on obtaining a "best estimate" of the mean number of animals present during each observation period with reference to each hour of the day and each tide subphase within that period. All are minimum estimates because some animals were probably missed at the seaward periphery of the study area. We tried to avoid inclusion of repeat sightings in these estimates which would lead to an upward bias, except where we calculated simple sightings of individuals per hour. The "best estimate" data were used to give relative abundance with respect to various environmental conditions, while sightings per hour were more appropriate for time-based comparisons such as relative abundance from year to year.

When sighting conditions were particularly favorable, the movements of specific groups were plotted, either by observation from one or other watch-stations which commanded a wide view with many landmarks, or by discreetly following them in the

kayak on a parallel course at distances of 50-150 m. If only one observer was present in the kayak, these periods were only included in the main data base if very few animals were known to be in the study area.

STATISTICAL ANALYSIS

For statistical analyses of these data we considered the potential application of log-linear and multivariate models, principle component analysis (PCA), factor analysis (FA), and a categorical data (χ^2) procedure. Considerable differences in the magnitude of x-variate variances would make results from PCA or FA suspect (Maxwell 1977, ch. 4). Log-linear and multivariate approaches were initially attractive, but both have disadvantages. Tests for independence of x-variates are difficult in the latter, and while these are facilitated by the former, results obtained from log-linear models are often difficult to interpret (SAS Institute Inc. 1979, p. 222). Furthermore, statistical advisers noted that use of the whole data base was contraindicated in either method because 1) there was of necessity inclusion of linear, nonlinear, and enumeration data types, and 2) there were significant numbers of empty data cells usually resulting from poor weather when operation would have been pointless. The consultants recommended use of the categorical data procedure, not only for the reasons outlined above, but also because the very nature of the x-variates (e.g., lunar cycle and tidal cycle) precluded the existence of complete independence. From the ecological point of view it was considered more important to relate one dependent variable (relative abundance of porpoises) to a group of variables one at a time than to test for independence in the latter when the result would likely be spurious.

We first determined ($P = 0.13+$) that no data set from any x-variate was significantly associated with one part of the "range" of any other by a series of simple paired χ^2 tests. The main analyses were then carried out on an IBM[5] 360 mainframe computer using the PROC FREQ program (SAS Institute Inc. 1979) which used a generalized least squares model to generate χ^2 values for combinations of the categorical levels between variables. In this case the relative abundance was related to date, time of day, tidal amplitude, tidal phase, lunar phase, extant wind direction, and wind direction 24 h previously.

To examine changes in spatial distribution within the study area, the location of 669 porpoise sightings collected in 1973-75 were plotted with respect to chronological time and time of tide. To avoid repeat sightings only the initial sighting was used in this context. To examine possible changes in distribution by depth and location, the study area was divided into three zones based on subsurface features: shallow shelving areas, subsurface slopes and scarps, and relatively deep basins and channels (Fig. 1). Such data cannot be used to deduce actual patterns of movement, but we were able to obtain some information on these through selective observations of identifiable individuals. Five of these were known to be females (consistently accompanied by calves), one a male (seen briefly copulating with a known female), and one of unknown sex. Each recorded sequential position was plotted for movements within a specific observation period, and for four of the known females data on all observations were plotted and the apparent ranges in consecutive seasons examined. In each case the master sheets had a grid with ordinates 100 m apart.

RESULTS

Hours of Observation of Porpoises in Fish Harbour Region

About 550 h of observation were made between June 1970 and September 1978, and 324 h of this were during an "intensive" study phase encompassing the summers of 1973-75. Estimates of changes in relative abundance with respect to environmental parameters were based on 181 h in optimal sighting conditions in this period (see section on Methods). Sporadic observations were maintained by our research group subsequent to 1975 or by auxilliary observers from Marine Research Associates of Lords Cove in most months except for late-December to mid-January.

Changes in Relative Abundance During the Year

From low relative abundance in the spring and late fall months, numbers of porpoises were highest during August or September in each year of the study period (Table 1). Highest values in ideal conditions were 8.00/h in Fish Harbour and 7.72/h in Simpson's Passage in September 1973 and August 1974 respectively. Observations by Marine Research Associates over the period 1971-77 in the same area, although largely of a casual nature, confirmed the animals can occur in small numbers in any month between Octo-

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sightings of harbor porpoises per hour in the Simpson's Passage and Fish Harbour areas, southern New Brunswick, 1970-78.

Month	1970	1971	1972	1973	1974	1975	1976	1977	1978
Simpson's Passage									
April	[1]0	—[2]	—	—	—	—	—	—	—
May	0.61 ± [3]0.07	0	—	0	—	—	—	—	—
June	0	0.90 ± 0.20	0.50 ± 0.15	0	—	—	—	0	0.94 ± 0.40
July	2.63 ± 0.30	1.91 ± 0.20	3.55 ± 0.40	3.55 ± 0.55	1.97 ± 0.65	1.68 ± 0.30	2.11 ± 0.30	0.76 ± 0.40	1.70 ± 0.25
August	4.42 ± 0.75	3.34 ± 0.60	6.44 ± 0.55	4.50 ± 0.60	7.72 ± 0.40	6.55 ± 0.40	3.37 ± 0.45	1.60 ± 0.25	1.93 ± 0.40
September	—	7.46 ± 1.15	6.33 ± 0.50	—	—	—	—	4.44 ± 1.00	7.47 ± 0.50
October	—	—	—	—	—	—	—	—	4.24 ± 0.02
November	—	—	—	—	—	—	—	—	0
Fish Harbour									
May	0	0	—	0	—	—	—	—	—
June	—	0	0	0.70 ± 0.01	—	—	—	0	0
July	0.93 ± 1.70	0.18 ± 0.05	3.44 ± 0.45	0.21 ± 0.04	0.46 ± 0.03	0.26 ± 0.04	0.92 ± 0.08	0.36 ± 0.15	0.22 ± 0.01
August	4.00 ± 0.78	1.04 ± 0.40	6.45 ± 0.40	4.48 ± 0.62	2.08 ± 0.70	1.94 ± 0.50	2.05 ± 0.30	1.17 ± 0.30	0.66 ± 0.08
September	—	2.41 ± 0.35	—	8.00 ± 1.80	5.22 ± 0.60	—	—	3.08 ± 1.12	0.89 ± 0.05
October	—	—	—	—	—	—	—	—	0
November	—	—	—	—	—	—	—	—	0

[1]No animals recorded. [2]No search effort. [3]Standard error of the mean.

ber and May, but probably rarely enter Fish Harbour (see next section).

Arrival and Departure of Porpoises Each Year in Relation to Sea Temperatures

First sightings in Fish Harbour were usually made in mid-late July when surface temperatures attained about 9°C, and never in Lords Cove until about mid-August despite 9°-11°C being reached at the surface in mid-late July. First regular sightings in Simpson's Passage varied from mid-May to late June. Determining the date of departure of the majority of animals from either sector was difficult because strong autumnal winds invariably interfered with observations from mid-September onwards when relative abundance was still high. In both 1977 and 1978, porpoises were still present in Fish Harbour until the last week of September and in Simpson's Passage until at least 15 October. Occasional animals may venture into the latter area in any month of the year since a very small population usually overwinters in the Quoddy region (Gaskin 1977), and one animal was sighted outside Fish Island on 7 December 1982 (B. M. Braune[6] and D. E. Gaskin, pers. obs.).

We could find no evidence that the distribution of porpoises was directly or indirectly influenced by the rather small daily local variations in sea temperatures within Fish Harbour. The most frequently observed known animal and her consorts would regularly traverse the width of the area (see Figure. 9) and their preferred locations appeared to have specific topographic rather than temperature characteristics.

Estimating Relative Abundance

Because the species does not make long dives (mean submergence 1 min 44 s, Watson and Gaskin (1983)), the required minimum period of observation needed to search the study area was not excessive. From our records we selected 3 wk in August 1972-75, when the probability of animals being present was high. In a random sample of 40 (i.e., above the minimum size for a "large" statistical sample (Bailey 1959)) search periods in optimum conditions of varying length (5 min to 2 h), the percentage of time that one or more animals was recorded increased from 50% for 10-min periods to well over 80% for 15-min periods. All observations of < 15 min were therefore discarded from the data set. If we were only interested in presence or absence, as in the case of simple locations at a given time of day or tide, observations from shorter periods or in Beaufort wind force 2+ were still of some value.

We have already outlined the methods for obtaining our "best estimates"; it is worth noting that various characteristics of the animals (e.g., short dive times, stereotyped movements, recognizable individuals) and of the study area (limited search area because of shallow water, many landmarks, shelter, and limited entry and exit points for animals) were of great assistance in reducing repeat sightings to a minimum.

[6]B. M. Braune, Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada.

Changes in Relative Abundance Between 1970 and 1978

Table 1 gives sightings of individuals per hour by month for each year from 1970 to 1978. As some observation periods were eliminated (see above) the results sometimes differ slightly from values given by Gaskin (1977) for the earlier years. Results suggest a decline in relative abundance from 1972 onwards in Fish Harbour and from 1974 onwards in Simpson's Passage. Because the 1970 values were based on a relatively short series of observations, the apparent rise from 1970 to 1971 may be spurious. The slight increase in 1978 is also suspect as most observers were less experienced than the teams used in 1970-77. The overall trend however, seems unmistakable. Furthermore, a decline in each month of the July-September period is evident when data for the whole study area are pooled (Fig. 2).

Results of the categorical data procedure tests for relative abundance of porpoises against the set of environmental parameters are presented in Table 2 (Fish Harbour) and 3 (Simpson's Passage). As might be expected, large χ^2 and significant P values were generated from the sharp drop in overall numbers sighted per observation period (regardless of its length) from 1972 to 1975, and from the great increase occurring each year between July and September. Time of day appeared to exert no influence on relative abundance in either section (P = 0.45, 0.20), nor was any statistically significant relationship noted between relative abundance and

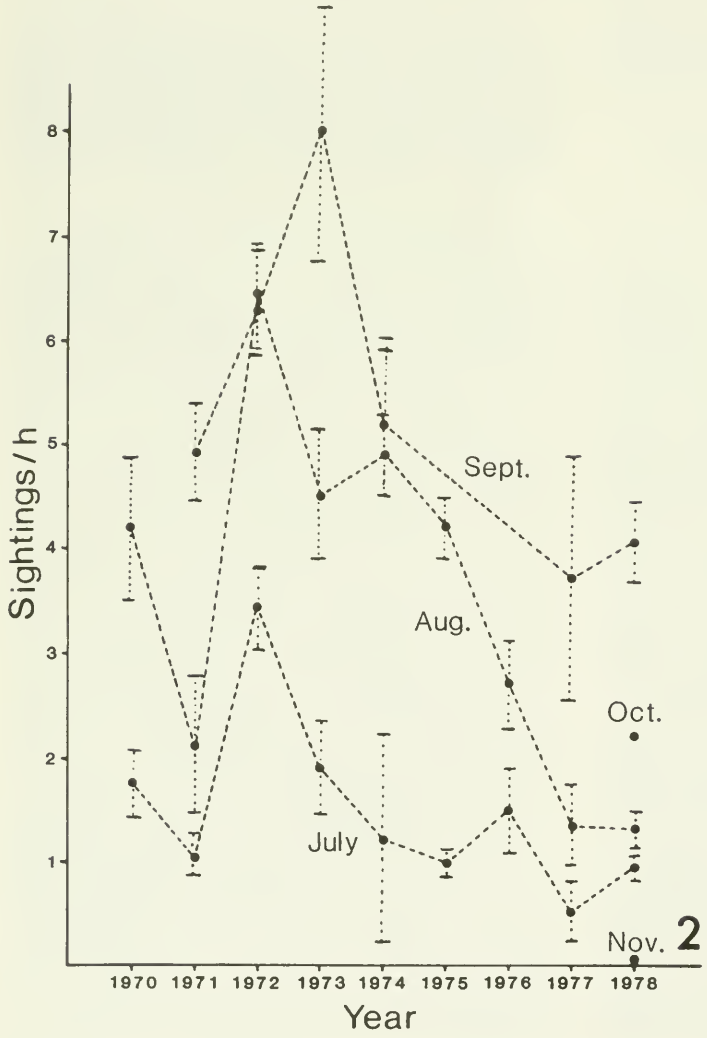

FIGURE 2.—Comparison of sightings per hour of porpoises in good condition in the Fish Harbour study area (Fish Harbour + Simpson's Passage), 1970-78 by month, from July to September. October and November values available for 1978 only. Vertical dots and bars represent standard error about the means.

TABLE 2.—Results of categorical data procedure tests for observed numbers of harbor porpoises in comparison to expected numbers with different environmental parameters in the Fish Harbour region of southern New Brunswick, 1972-75. I. Fish Harbour + Lords Cove (see Figure 1). n = observation periods; χ^2 = two-way table statistic.

Parameter measured	n	df	χ^2	P
Years (1972-75)	249	3	39.57	0.0001*
Time of year[1] (July to early September)	249	2	63.69	0.0001*
Time of day[2] (0600- + 1900)	249	4	3.67	0.4520
Tidal amplitude[3]	249	3	7.80	0.0500*
Tidal phases[4] (Start of falling tide to end of rising tide)	249	7	3.31	0.8450
Lunar phase[5] (New moon to full moon)	249	3	5.38	0.1450
Wind extant[6] (On shore, coastwise, or offshore)	249	2	17.58	0.003
Wind 24 h previous[6]	249	2	12.22	0.0094

[1]Categorical division of three periods (July, first 3 wk of August, last 1½ wk of August + early September) to balance effort.
[2]Four periods of 3 h each, post-1900 observations amalgamated.
[3]Four subphases (≥ 5.5, 5.6-6.5, 6.6-7.5, ≥ 7.6 m).
[4]The eight subphases given in Figure 4 were used.
[5]Three subdivisions used. More subdivision than these resulted in many empty data cells.
[6]Four subdivisions used. More subdivision than these resulted in many empty data cells.
*Statistically significant at 0.05 level or better.

TABLE 3.—Results of categorical data procedure tests for observed numbers of harbor porpoises in comparison to expected numbers with different environmental parameters in the Fish Harbour region of southern New Brunswick, 1972-75. II. Simpson's Passage. n = observation periods; χ^2 = two-way table statistic.

Parameter measured	n	df	χ^2	P
Years (1972-75)	132	3	7.58	0.050*
Time of year[1] (July to early September)	132	2	16.99	0.0002*
Time of day[2] (1600- + 1900)	132	4	5.98	0.201
Tidal amplitude[3]	132	3	2.54	0.468
Tidal phases[4] (Start of falling tide to end of rising tide)	132	7	9.97	0.190
Lunar phase[5] (New moon to full moon)	132	3	7.38	0.061**
Wind extant[6] (Onshore, coastwise or offshore)	132	2	0.95	0.620
Wind 24 h previous[6]	132	2	0.93	0.628

[1]Categorical division of three periods (July, first 3 wk of August, last 1½ wk of August + early September) to balance effort.
[2]Four periods of 3 h each, post-1900 observations amalgamated.
[3]Four subphase (≥ 5.5, 5.6-6.5, 6.6-7.5, ≥ 7.6 m).
[4]The eight subphases given in Figure 4 were used.
[5]Three subdivisions used. More subdivision than these resulted in many empty data cells.
[6]Four subdivision used. More subdivision that these resulted in many empty data cells.
*Statistically significant.
**Close to significance at 0.05 level.

magnitude of tidal amplitude in Simpson's Passage. In shallower, semi-enclosed Fish Harbour however, significantly more porpoises were present (P = 0.05) at low tidal amplitudes (≤ 6.5 m) than high amplitudes (≥ 6.6 m). Data for the most commonly sighted individual (a female with a large dorsal scar) corroborated this general finding; about 78% of all sightings of this animals were made when the amplitude was 6.5 m or less.

Relative abundance did not alter (P = 0.84, 0.19) in either zone of the study area during the tidal cycle. Similarly no significant change occurred relative to the lunar phase in Fish Harbour, although in Simpson's Passage the χ^2 value approached the arbitrary 0.05 level of significance (P = 0.061; n = 249). No relationship between extant or previous wind direction was evident in Simpson's Passage (P = 0.62, 0.63; n = 132), but there appeared to be a significant association between wind direction and relative abundance of porpoises in Fish Harbour (P = 0.0003, 0.009; n = 249). In both cases far more animals were present during onshore wind directions than when winds were coastwise or offshore.

Distribution and movements of porpoises on the fine scale is likely to be correlated with the presence or absence of food species which, in the Quoddy region, consist largely of juvenile herring, *Clupea harengus*; mackerel; and small gadoids (Smith and Gaskin 1974). The dispersal of the former in this region is greatly influenced by current velocities (Jovellanos and Gaskin 1983). Unfortunately the beam width of available equipment was far too narrow to permit us to cover the study area by acoustic survey thoroughly, or even representatively, at any given time or tide phase. Because one of our major aims at the outset of the study was to avoid disturbing normal behavior of the porpoises, it was also rarely possible to acoustically scan in their immediate vicinity. We were however able to infer feeding behavior from diving patterns (e.g., "pattern B") carried out consistently in one location (Watson and Gaskin 1983). Sometimes fish were seen jumping at the surface in such areas (Fig. 3), and these zones were acoustically scanned on an opportunistic basis. Fish schools, recorded during bottom topographic acoustic mapping runs, tended to be concentrated at several locations in which porpoises were often sighted. Usually these traces were of herring school-type. While this species predominates in the Quoddy region in the summer months (Jovellanos and Gaskin

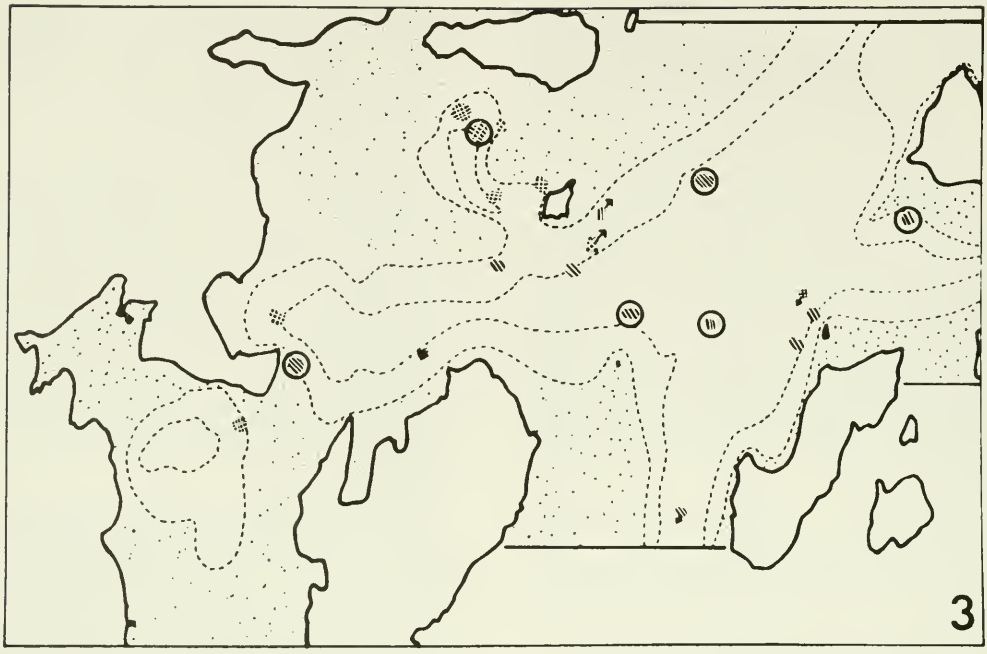

FIGURE 3. – Locations in Fish Harbour at which fish were detected visually or by sonar in 1973-78; opportunistic records only. Stipple: species not identified; vertical bars: Atlantic mackerel; diagonal bars: Atlantic herring; circles: one or more porpoises simultaneously present with record; arrows: direction of fish movement. The size of hatched areas indicates approximate size of the school.

1983), some could have been of harbor pollack, which are also taken by this species.

Changes in Distribution Within the Fish Harbour Region

No differences in distribution of the 669 recorded sighting positions for 1973-75 could be detected when they were plotted either by four or eight time periods from 0600-2200, but considerable differences were evident when they were plotted against eight subphases (slack low, slow flood #1, fast flood, slow flood #2, slack high, slow ebb #1, fast ebb, and slow ebb #2) of the tidal cycle. This analysis ignores for the moment the fact that many animals move in a rather regular manner through the study area, since useful information can be obtained simply from noting where they are at any given time of tide. The results (Fig. 4) showed that up to 80% of porpoises were congregated over the shallow shelf margins, slopes, and scarp areas between the onset of flood tide and high water. Conversely, about the same proportion became concentrated over the basin and channel areas between onset of the ebb, and slack low water.

The Nature of Movements Within the Fish Harbour Region

It became evident that when the recognizable animals returned each year they reestablished "specific ranges" (for lack of a better term) in virtually the same locations in Fish Harbour each summer (Figs. 5-8). There is some evidence that these "ranges" shifted progressively further east of Deer Island between 1973 and 1975, especially in the case of the scarred female mentioned earlier. Each of these areas in Fish Harbour, of which we were able to measure nine approximately, appeared to be about 1.0-1.5 km^2 in extent. Even the most distinctive animals would disappear from the study area for extended periods and then reappear again, just as Gaskin et al. (1975) noted for a female carrying a radiotelemetric package. The scarred female was once observed with a calf off the eastern coast of Simpson's Island, and on another occasion between Minke Ledges and Tinker Island, which lie between 1 and 3 km south of the main study area. This specimen was present in the Fish Harbour region for about half the days of excellent visibility in 1973-75, was well known to all observers, and yet was only

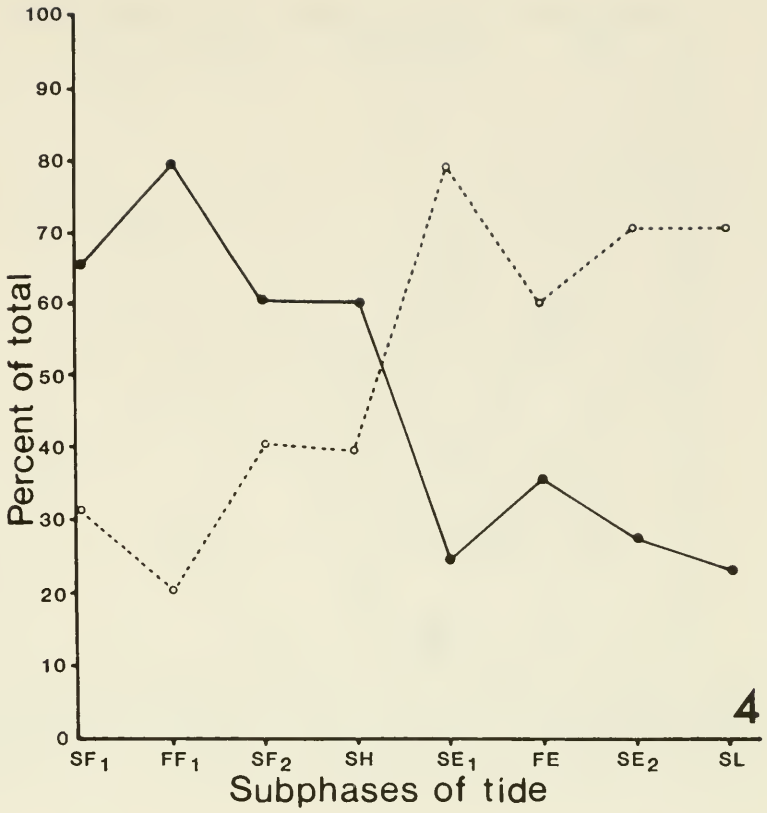

FIGURE 4.–Distributions of 669 harbor porpoises in Fish Harbour 1973-75 over subsurface topographic features, by eight subphases of the tide: Slack low water (SL), slow flood 1 (SF_1), fast flood (FF), slow flood 2 (SF_2), slack high water (SH), slow ebb 1 (SE_1), fast ebb (FE), and slow ebb 2 (SE_2). Solid line shows percentage over shallow shelf, scarps, and slopes; dotted line, percentage over basins and channels.

seen on the two above occasions during simultaneous surveys outside the present study area.

Only in the case of this particularly distinctive animal were we able to obtain enough observations to map some of her patterns of movement over extended periods. On 17 August 1973, for example, we tracked her for 2 h 12 min (57 position fixes, Fig. 9), noting that she tended to stay close to the slopes of the main basin-channel, with one foray around the small basin in Lords Cove. This kind of point-to-point travelling interspersed with short periods of submergences in one location is quite typical of this species. This animal repeated almost identical range movements on 13 and 29 August 1974. On 1 and 30 August 1974 (1 h 4 min and 3 h 3 min respectively) this animal spent far longer periods in relatively restricted locations (Fig. 10). Submergences were again of the "pattern B" type, and no surface resting was recorded. On 1 August many herring were seen jumping at the surface immediately after each submergence by the female. Her calf was often left at the surface during these bouts.

"Systematic patrolling" of small areas, often in the lee of ledges or small islets was also recorded (Fig. 10). The movements illustrated were carried out by a school of three medium-sized animals accompanied by one small one on 2 August 1974. The group sychronously dove repeatedly while moving back and forth in one restricted scarp location, then abruptly travelled to the second location shown and repeated the pattern.

DISCUSSION

The distribution of some small odontocetes is known to be correlated with sea surface temperatures (Gaskin 1968; Würsig and Würsig 1980), but the relationship is almost certainly indirect, the result of influences exerted one or more levels further down the food chain. The entry of the main summer population of harbor porpoises into the study area not only coincides with 9°-10°C surface temperatures, but also with the arrival of large numbers of juvenile herring which feed in the Quoddy region during the summer months (Battle et al. 1936; Jovellanos and Gaskin 1983). Although transport of relatively small fish into the study area might be expected to be at a maximum during spring tides,

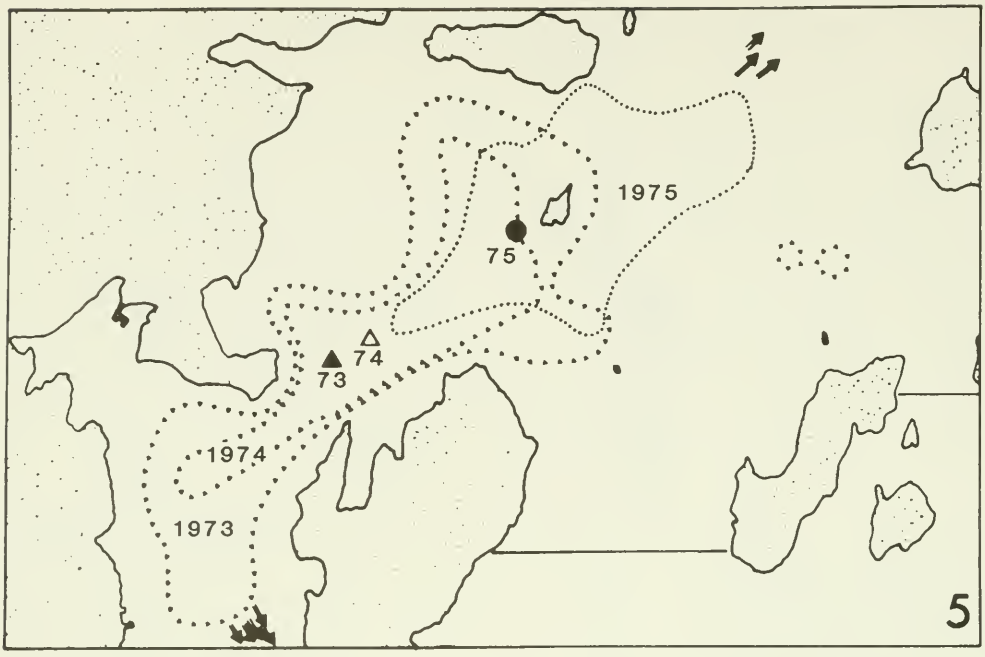

FIGURE 5.—Broken lines encompass all sightings of recognizable animal (#1, scarred mother). 1973: solid wedges; 1974: open wedges; 1975: dots. The solid triangle, open triangle, and solid circle respectively represent the center of the "range" as determined by the mean of the latitudes and longitudes of each position, excluding single isolated sightings. Arrows indicate number of times this animal (and any consorts) were observed leaving the "range". In each case they were swimming at 4+ knots and outdistancing the kayak.

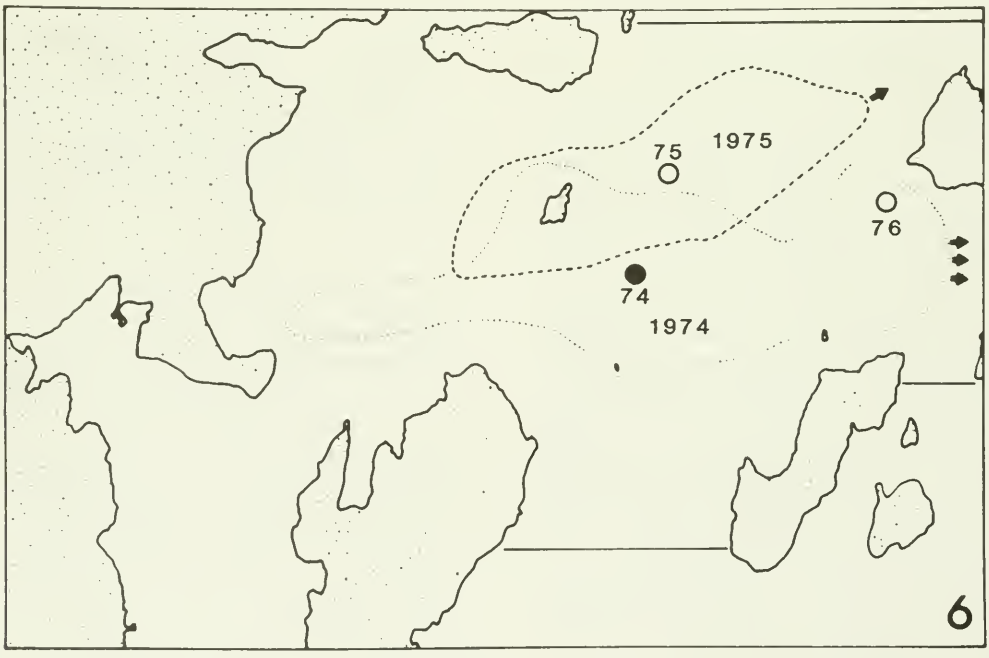

FIGURE 6.—Broken lines encompass all sightings of known animal #2 (clipped fin). 1974: dotted lines; 1974: dashes. Open circle and closed circle for 1974 and 1975 respectively, and arrows indicating animal leaving the area are as in Figure 5.

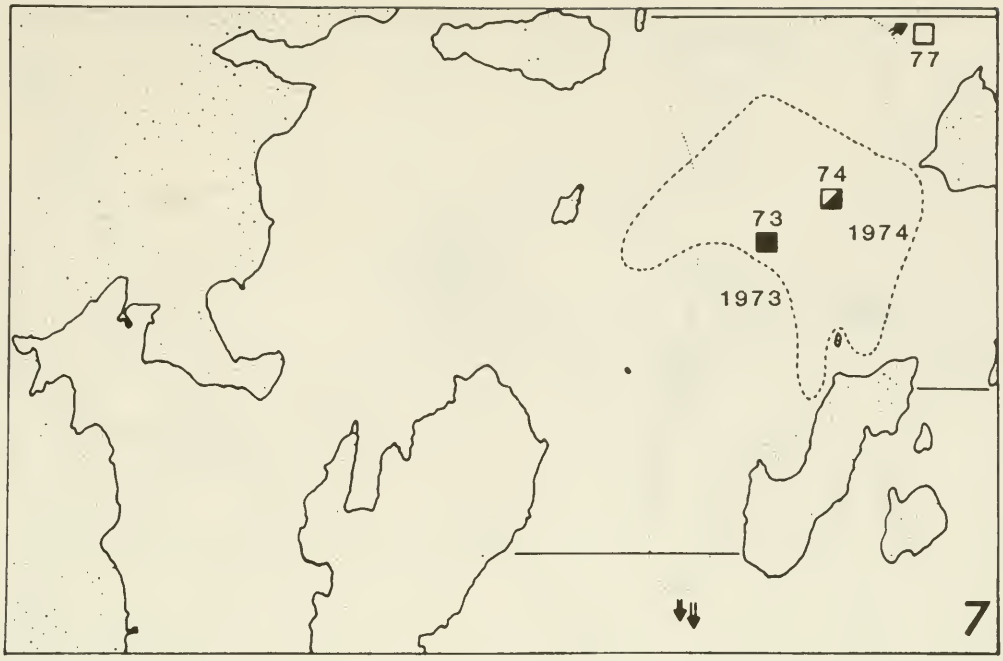

FIGURE 7. – Broken lines encompass all sightings of known animal #3 (Simpson's Passage mother) except for single 1977 sighting. 1973: dotted line; 1974: dashed line. Other symbols as in Figure 5.

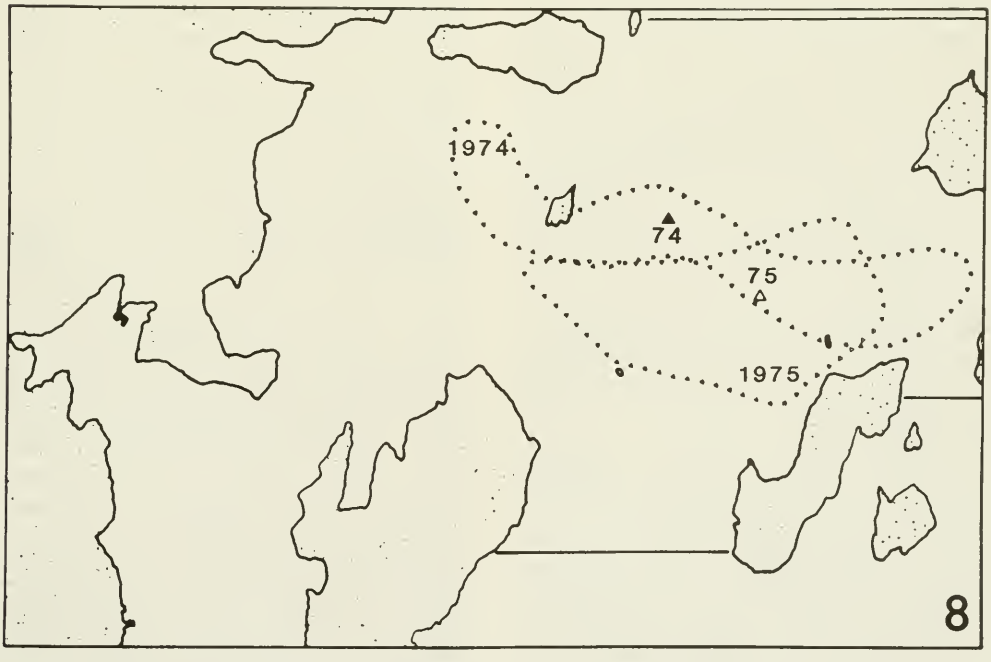

FIGURE 8. – Broken lines encompass all sightings of known animal #4 (Light brown mother). 1974: solid wedges; 1974: open wedges. Other symbols as in Figure 5.

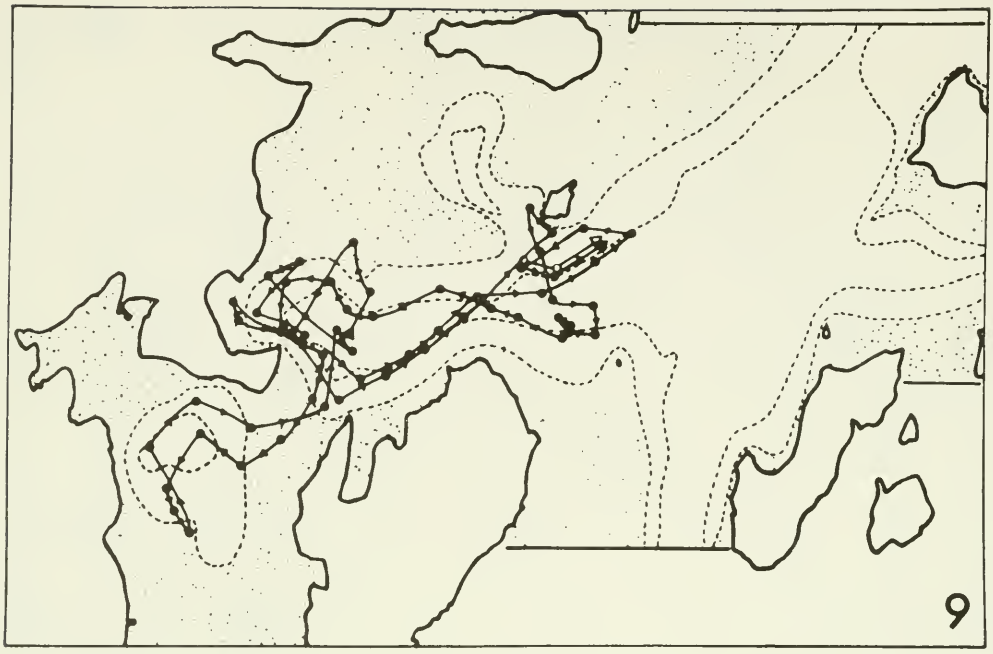

FIGURE 9.—Movements of scarred mother during 2 h 12 min period of 10 August 1973 accompanied by calf (57 position fixes). On some occasions they resurfaced close to an immediately previous position; about 75 surfacings are represented by these positions. Reverse arrow indicates initial contact point (just outside Lords Cove), solid arrow point where tracking was abandoned, and white circles position of a medium-sized animal which briefly joined the pair.

we found relative abundance of porpoises conversely to be greatest during neap tides. About 63% of the sightings in 1973-75 were of mothers and calves. Possibly these animals stay out of semi-enclosed areas during periods of maximum water transport, especially in areas with turbulent shallows such as the Fish Harbour region. On the other hand, if there are larger numbers of herring schools moving into the outer part of the Quoddy region it may not be necessary to forage in inshore waters. Once the animals are in the study area however, the observed changes in distribution during the tidal cycle confirm the earlier subjective comment (Watson 1976) that porpoises seemed to move inshore with the flood tide and offshore with the ebb.

The distribution of porpoise activity in the region appeared to be closely related to subsurface topography, particularly the margins of the basins and channels in areas of restricted water flow, the lee of islets, especially Fish Island and the Nub, and blind trench heads such as that just north of Hathaway Head. Because our meager acoustic records revealed fish traces in all these sites at one time or another (Fig. 3), we speculate that these may be areas of fish accumulation which the porpoises have learned to exploit. Each may have subsurface eddies or areas of relatively slack water against the lee side of the slope or near the bottom, in which fish can shelter from strong currents, and in which zooplankton might also accumulate. In such areas fish could not only avoid being carried further inshore, but could also feed (Hamner and Hauri 1977). Dispersal from offshore areas into the coastal belt is likely to be augmented by onshore winds, which can increase significantly the flow of water in the immediate surface layers. Local fishermen believe that offshore winds serve to hold "feed" away from the coast, while coastwise winds might reduce the possibility of entry into Fish Harbour by increasing surface flow past the relatively narrow passages. We conclude that light or moderate winds are unlikely to affect any small cetacean directly; when winds were strong enough that behavior might conceivably be affected, we were not usually operating.

Large variation always occurs in data such as these, and it is to a large extent unpredictable. Such variation in relative abundance can be explained quite simply; these animals are large, highly mobile predators with sophisticated adaptations both for active and passive acoustic scanning for their equally

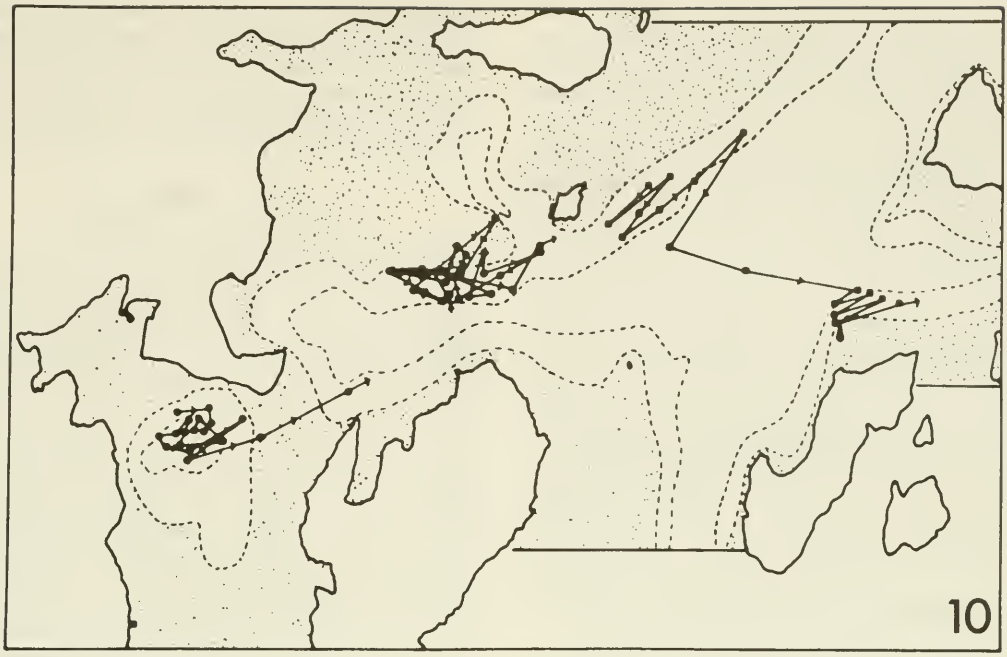

FIGURE 10. – Movements of scarred female on 30 August 1974 (solid circles at left of figure) and 29 August 1974 (solid circles in center of figure). Solid squares show "patrolling" behavior of school of four animals recorded on 2 August 1974. Qualifying comments on position fixes and surfacings in Figure 9 apply here also.

mobile prey. That the harbor porpoises in this area can shift tens of kilometers in a few hours cannot be questioned (Read and Gaskin in press); if few fish are present in one area, they may well move in a loosely synchronized group to forage in other localities. This degree of mobility and scanning ability is highly adapted not only to the mobility of their prey species, but also to the patchy nature of the distribution patterns of such fish; there is probably a significant random element in the dispersal of juvenile herring in the Quoddy region (Jovellanos and Gaskin 1983). The type of porpoise movement shown in Figure 9 was presumed to indicate that prey were dispersed, since the animal spent little time in any one location. In the other movement pattern (Fig. 10) the same animal was believed to be encountering prey in local concentrations that merited prolonged submergences in one area.

We have little evidence that the region might be significant either as a mating area or a calving ground. Females appear to have their calves offshore, since, although the latter may be very small in late June and July, they already accompany females sighted in the outer part of the Quoddy region (Smith and Gaskin 1983). Many females with calves appear to remain on tidal convergence streaks up to 20 km offshore in the outer Quoddy region (Read 1983) and may not move into the coastal zone at all. It seems more likely that the study area functioned as a significant feeding area for this species rather than being a zone favoured for reproductive activity.

The demonstrated existence of "specific ranges" and annual returns by individual harbor porpoises in this study is not surprising. Rather similar patterns, although sometimes on very different geographical scales, have been recorded for *Delphinus delphis* by Martin et al. (1971), *Orcinus orca* by Bigg (1982), *Tursiops truncatus* by Wells et al. (1980) and Würsig and Würsig (1979), and *Lagenorhynchus obscurus* by Würsig and Würsig (1980). Periodic disappearances and abrupt reappearances of *T. truncatus* were also recorded by Würsig (1978), while studying the animal.

With respect to the progressive decline in relative abundance in the peak part of summer, lack of consistent observations through late September-late October (because of high winds) prevented us from determining whether or not this resulted from a real population decrease in the area, or simply a shift of peak abundance from mid-August to mid-September during the decade. Consequently we adopted an indirect approach to the problem, plotting sightings

per hour for each month of summer for each year with sufficient data (Fig. 2). This suggests that the decline resulted from a combination of both factors, with a general overall decline in relative abundance since about 1973 and a progressive retardation of the peak of numbers since about 1975. Unfortunately there is insufficient information in Department of Fisheries and Oceans records to decide if any change in food supply could have occurred during those years, especially with respect to juvenile herring abundance (T. D. Iles[7]). Nevertheless, our surface temperature records for the inner Quoddy region reveal a consistent decline in the mean summer value (centered on mid-August) from above 12°C in 1971 to below 11°C in 1977 (Gaskin et al. 1979). The temperature curve is compared with the pattern of relative abundance in Figure 11; there is close correspondence from 1972 onwards. Such a decline might result from increase in relative dominance of Nova Scotia current water in the Bay of Fundy (Sutcliffe et al. 1976) and perhaps a significant decline in the availability of zooplankton prey of juvenile herring. Alternatively the slightly cooler waters might be marginally less suitable for young porpoise calves.

[7]T. D. Iles, Biological Station, Department of Fisheries and Oceans, New Brunswick, E0G 2X0, Canada, August 1980.

ACKNOWLEDGMENTS

The authors are very grateful to J. Hines and G. Darlington of the Department of Mathematics and Statistics at the University of Guelph for much assistance and advice during the analysis of the environmental data. G. J. D. Smith and A. J. Read of the Department of Zoology read the manuscript in its several drafts, and along with two anonymous referees gave much useful and constructive advice regarding improvements. Many former and current assistants and graduate students, too numerous to name, helped to collect the laboriously obtained field data. Marine Research Associates of Lords Cove and the late R. Thurber of St. Andrews, N.B., provided

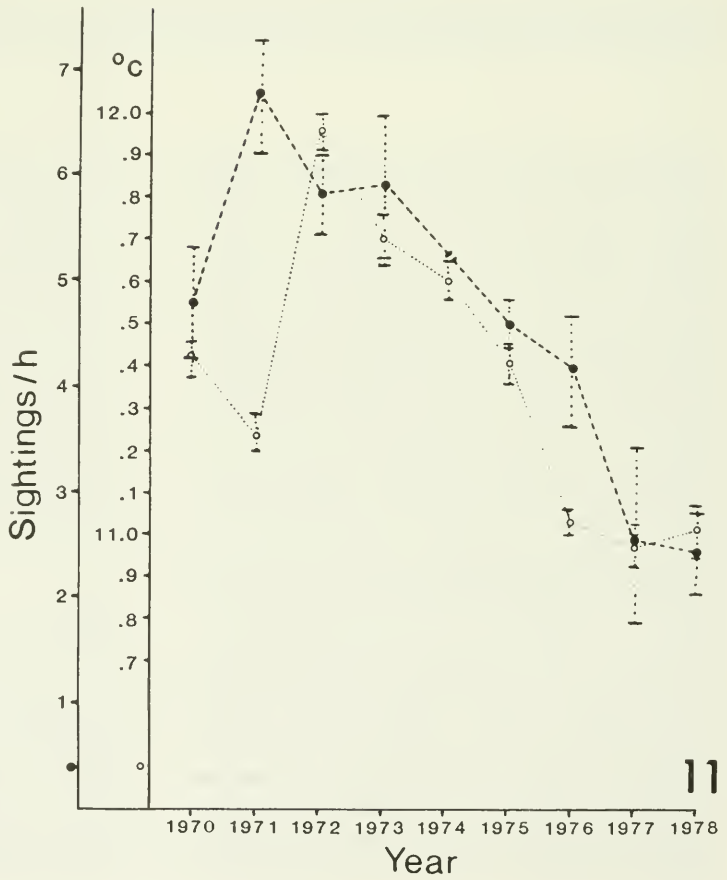

FIGURE 11.—Comparison of midsummer (late July-early September) sightings per hour of harbor porpoises in the Fish Harbor region of New Brunswick between 1970 and 1978 with surface temperatures based on 8 stations (n = about 60/annum): Solid circles and dashed line (sightings per hour), open circles and dotted line (°C). Vertical dots and bars represent the standard error about the mean.

valuable logistic support. The program was funded through Natural Sciences and Engineering Research Council of Canada operating grant A8563 throughout, and in later stages by a subvention from Fisheries and Oceans Canada and a grant from the Canadian National Sportsmen's Fund.

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THE RELATIONSHIP BETWEEN TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, ABUNDANCE AND SEDIMENT COMPOSITION OFF GEORGIA

Elucidation of the relationship between physicochemical factors and fish abundance has long been of interest to fisheries biologists. For example, water temperature frequently exerts a strong influence on the abundance of many pelagic marine fishes (Radovich 1961; Laurs et al. 1977; Barkley et al. 1978; Moyle and Cech 1982), and this effect has been noted also for freshwater species (Magnuson et al. 1979; Moyle and Cech 1982). For benthic marine fishes, however, substrate composition may be a more important factor affecting fish abundance and distribution. Associations between abundance and substrate composition have been noted for a diverse group of fishes: agonids, bothids, cottids, pleuronectids, scorpaenids, and steichaeids (Day and Pearcy 1968; Powell and Schwartz 1977; Marliave 1977; Barton 1982). Where detectable, however, these associations vary substantially in intensity. This is probably due to the fact that many physicochemical factors are intercorrelated and most fishes probably respond to intercorrelated suites of variables rather than to single factors alone.

In this note we quantify the relationship between catch rate of a demersal species, the tilefish, *Lopholatilus chamaeleonticeps*, and substrate composition. This species is commercially exploited throughout most of its range (Grimes et al. 1980; Low et al. 1983; Turner et al. 1983), although, prior to this study, tilefish resident to the continental slope off Georgia appeared to have been subjected to minimal exploitation (D. Harrington[1]). The elucidation of a substrate-abundance relationship for tilefish should aid in the management and harvest of this species.

Methods

A total of 19 bottom longline sets and 19 sediment samples were obtained during daylight hours, between 5 May and 22 November 1982. Fourteen longline sets, each comprising 1.6 km of line, and 12 sediment samples (Table 1) were obtained from the RV *Georgia Bulldog* (University of Georgia Sea Grant Program vessel). Five sets ($\bar{X} \pm 1$ SD length = 0.31 $\pm$ 0.09 km) and seven sediment samples were collected aboard the RV *Delaware II* (National Marine Fisheries Service vessel). At least one of the authors was present during collections.

Bottom longlining on the *Georgia Bulldog* was conducted using snap-on gangions ($\sim$ 0.5 m in length) spaced about 4 m apart, along a 6.3 mm diameter galvanized aircraft cable groundline. Gangions were equipped with 4/0 or 5/0 circle hooks and baited with either fish or squid. A similar system was employed on the *Delaware II* except that a much shorter groundline of 6.3 mm diameter hardlaid nylon was used (Table 1), with hook sizes ranging from 3/0 to 8/0.

Substrate Analysis

Substrate samples were collected with a 25 $\times$ 30 $\times$ 37.5 cm box dredge suspended from a power winch. The dredge was lowered to the bottom and then dragged across the substrate (typically for < 5 min). After retrieval, 1.2-2.0 kg of sediment were removed from the dredge and stored in plastic bags. It is assumed that these samples accurately reflect the composition of surface sediments.

Sediment samples varied in their proximity to longline sets. Fourteen samples were taken at the end of longline sets. Of the remaining five samples, one was taken from the midpoint of a set, three were taken alongside sets within a distance of 0.2 km, and one was taken alongside a set at a distance of 0.6 km. The general area sampled (see Table 1 for loran C coordinates) has a relatively homogenous, low-relief bottom topography, and large variations in substrate composition probably do not occur over short distances (V. J. Henry[2]).

To determine the fraction of each sample composed of sand and silt-clay, a known amount of sediment (i.e., enough to yield a dry weight of between 60 and 100 g) was dried in a forced-air oven at 98°C until a constant weight was reached. The sample was then moistened with water which contained $\sim$ 2 g of Calgon[3] as a dispersant, and washed through a sieve which retained particles $\geq$ 0.0625 mm (4ϕ) (U.S. standard seive #230). Sediments retained by the sieve were then oven-dried to a constant weight to

[1]D. Harrington, University of Georgia Marine Extension Service, Brunswick, GA 31523, pers. commun. 1983.

[2]V. J. Henry, Dept. of Geology, Georgia State University, Atlanta, GA 30303, pers. commun. 1983.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sediment composition and catch data for longline sets used to establish the relationship between catch rates and sediment composition off Georgia.

Date	Loran C coordinates	Minimum and maximum depths (m) of longline sets	Groundline length (km)	Number of hooks	Soak time (h)	Tilefish per 100 hook-h^{-1}	Percent sand (≥4ϕ)	Percent silt-clay (<4ϕ)
5-5-82	45086.1 60777.3	187-190	1.61	242	3.3	2.11	[1]58	42
5-29-82	45092.9 60743.2	193-194	1.61	390	4.3	1.72	53	47
5-29-82	45093.8 60729.9	[2]196	1.61	348	5.3	3.29	[1]49	51
5-30-82	45088.0 60869.4	140-143	1.61	284	3.5	0	85	15
5-30-82	45080.8 60864.2	164	1.61	330	4.2	0	69	31
5-30-82	45076.8 60854.7	182-185	1.61	247	4.0	0.41	64	36
5-30-82	45073.0 60847.0	203	1.61	254	3.6	0	64	36
5-30-82	45069.6 60841.0	219	1.61	298	2.9	0.57	79	21
6-29-82[3]	44736.5 61531.7	No data	0.18	50	2.5	0	88	12
7-1-82[3]	45039.6 60974.6	199	0.35	100	2.0	0	69	31
7-2-82[3]	45065.4 60868.6	No data	0.35	100	1.0	0	80	20
7-12-82[3]	26979.6 39551.5 (9960-chain)	216-223	0.35	103	1.0	0	98	2
7-24-82	45109.8 60548.5	186-187	1.61	258	3.2	3.56	[1]40	60
7-25-82	45101.0 60549.0	217-219	1.61	241	4.0	3.80	48	52
8-13-82	45076.0 60842.6	195-201	1.61	266	3.0	0.50	74	26
8-14-82	45085.6 60735.0	230	1.61	352	3.7	2.98	57	43
8-17-82	45093.8 60555.9	255-258	1.61	245	3.9	1.67	55	45
11-22-82	45097.8 60720.5	186	1.61	311	3.5	3.95	[1]48	52
11-22-82	45095.8 60716.0	189-191	1.61	250	2.9	5.34	52	48

[1]Substrate samples were taken during a different cruise, however, samples were always taken within 65 d of each other.
[2]A single depth measurement means that only one reading was taken during the longline set. This depth is an approximation of longline depth.
[3]Samples taken from the *Delaware II*.

determine the percentage of sand and larger particles in the sample. The silt-clay fraction was obtained by subtraction. Replicate subsamples were taken from six collections to establish the technique's precision. The mean difference in percent silt-clay fraction among the six replicates was 2.5% (s = 1.4%). A t-test for paired samples indicated that significant differences did not exist among replicate determinations for a given sample (t = 0.30, df = 5, $P > 0.7$).

Statistical Analysis

To determine the relationship between tilefish catch rate and sediment composition, we used the silt-clay fraction of each substrate sample as an independent variable (X) and catch rate (i.e., tilefish caught/100 hook-h per soak time) as the dependent variable (Y). Exponential and polynomial regression models were fit to the data using the SAS statistical programs (SAS Institute Inc. 1982). The best polynomial model was compared with the nonlinear exponential model using R^2 as the criterion for model performance. Similar patterns of variation were observed in plots of residuals from all models, hence R^2 values are a reasonable criterion for model selection.

Results

The size structure of tilefish caught off Georgia was typical of unexploited to lightly exploited tilefish stocks (Grimes et al. 1980; Turner et al. 1983). This size structure remained relatively constant for ~ 10 mo, after which a slight decrease in catch rates and a possible truncation of size structure were observed (authors' unpubl. data). These results confirm verbal reports that little exploitation has occurred off Georgia (Harrington footnote 1). Hence, the data used in this analysis were probably not influenced by prior exploitation.

A total of 323 tilefish were taken on 19 longline sets (Table 1). Catch rates ranged from 0 to 5.34 tilefish/100 hook-h. Parameter estimates for linear and quadratic terms of the polynomial regressions were significantly different from zero (Table 2). Inclusion of a cubic term, however, did not significantly improve ($F = 0.75, P > 0.40$) the fit which was obtained using a second-degree polynomial. The second-degree polynomial yielded a higher R^2 value than the nonlinear exponential model (Table 2) and hence was deemed to be the model of best fit. The y-intercept of this model also was not significantly different than zero (Table 2, Fig. 1) which contributes to its biological realism. Using this equation, 74% of the variation in catch rate could be accounted for by substrate composition alone.

TABLE 2.—Comparison of regression models. Either F-tests (b_1), t-tests (b_0), or asymptotic confidence intervals (exponential model) were used to test the significance of parameters.

Model	b_1	b_0	R^2
$y = 0.087X - 1.496$	**	*	0.64
$y = 0.155(e^{0.058X})$		*	ns 0.68
$y = 0.002X^2 - 0.050X + 0.122$	***	ns	0.74

ns = nonsignificant
* = $P < 0.05$
** = $P < 0.001$
*** = $P < 0.0001$

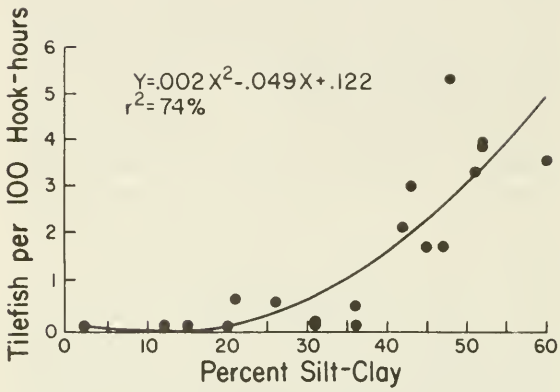

FIGURE 1.—Relationship between the silt-clay fraction of the sediments and tilefish catch rates off Georgia, U.S.A.

Discussion

Tilefish abundance, as estimated by catch rates off Georgia's continental slope, was strongly correlated with the silt-clay fraction of the substrate. This relationship was nonlinear, and based on R^2 values, a second-degree polynomial regression provided the best fit to the data. Off the northeastern United States, tilefish also were most abundant on fine-grain sediments (Able et al. 1982), although they were also found in horizontal burrows in the sides of submarine canyons (Warme et al. 1977), and in boulder fields (Valentine et al. 1980). Because tilefish construct vertical burrows in the substrate (Able et al. 1982), they require sediments which possess sufficient stability to prevent the collapse of their burrows. It would appear that bottom areas off Georgia which contain a sand fraction > 60% do not support substantial tilefish densities (Table 1, Fig. 1). It is likely that such substrates are not stable enough to allow tilefish to construct burrows. Thus, the observed correlation between catch rate and substrate composition has a biologically realistic explanation: substrates with high silt-clay fractions are conducive to the construction and maintenance of tilefish burrows, while substrates with high sand fractions are not. A similar explanation, based on submarine observations, has been proposed by Able et al. (1982) to explain tilefish distributions off the northeastern United States. Although we have not observed tilefish burrows off Georgia, they have been identified in soft bottom areas off South Carolina (R. Jones[4]).

While the relationship between catch rates and sediment composition is quite strong, several potential sources of error exist in our data. First, catch rate data were collected from two different vessels using different gear. Pooling data from the different vessels, however, would tend to obscure the relationship between catch rates and sediment composition. Hence, if differences in sampling methods did have an effect on our data, it would make the estimates of the catch rate-sediment relationship conservative.

Second, only one substrate sample was collected with each longline set. While quantification of

[4]R. Jones, Harbor Branch Foundation, Fort Pierce, FL 33450, pers. commun. 1983.

geographical variation in substrate composition was beyond the scope of this project, low relief areas off Georgia generally do not display large variations in substrate composition (Henry footnote 2). Evidence to substantiate this point is presented in Table 1, as substrate samples from areas with similar loran coordinates typically possessed similar substrate compositions.

Third, while a seasonal component to catch rate has been observed off New Jersey (Grimes et al. 1980), our data for this analysis do not strongly display this trend (Table 1).

In addition, because the area fished did not display evidence of significant prior exploitation, our results were not affected by the potentially confounding influence of commercial fishing.

In conclusion, approximately three-quarters of the variation in tilefish catch rate off Georgia could be attributed to variation in a single physicochemical factor: the silt-clay fraction of the substrate. At present, however, the generality of this relationship is unknown with respect to other geographical areas or locations with different exploitation histories. In addition, temperature also has been shown to affect the distribution of tilefish off the northeastern United States (Grimes et al. 1980). It is likely that within areas possessing suitable thermal regimes, substrate composition is a major factor affecting tilefish abundance. While a variety of associations between fish abundance and physicochemical factors have previously been identified (Moyle and Cech 1982), to our knowledge, none approach the intensity of the relationship described herein. We believe that identification of this relationship will aid fisheries biologists in the identification and demographic quantification of tilefish stocks as well as the location of new fishing grounds.

ACKNOWLEDGMENTS

We appreciate the assistance of the captains and crews of both the *Georgia Bulldog* and the *Delaware II*, without whom this work would not have been possible. The following individuals either reviewed the manuscript or aided in other aspects of the study: K. Able, C. Barans, P. Bartlett, E. Chin, D. Beaumariage, D. Daniels, D. Erickson, M. Freeman, S. Floyd, C. Grimes, E. Guthertz, D. Harrington, V. Henry, J. Hill, B. Low, L. Parker, L. Pittman, M. Rawson, D. Stouder, G. Ulrich, and C. Wenner. Facilities and logistic support for this study were graciously provided by the University of Georgia Marine Extension Service at Brunswick. We also wish to acknowledge the continued support of our research by the Georgia Sea Grant College Program under contract #NA80AA-D-00091. The manuscript was ably typed by Bonnie Fancher.

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Gary D. Grossman
Michael J. Harris
Joseph E. Hightower

School of Forest Resources
University of Georgia
Athens, GA 30602

THE DEVELOPMENT AND OCCURRENCE OF LARVAE OF THE LONGFIN IRISH LORD, *HEMILEPIDOTUS ZAPUS* (COTTIDAE).

The subfamily Hemilepidotinae, endemic to the North Pacific Ocean, is one of the more generalized subfamilies within the Cottidae (Peden 1978). According to Peden (1978), the subfamily is composed of three subgenera: 1) *Calycilepidotus* which includes *Hemilepidotus spinosus*; 2) *Hemilepidotus* which includes *H. hemilepidotus*, *H. jordani*, *H. zapus*, and *H. gilberti*; and 3) *Melletes* which includes *H. papilio*. The early life histories of most species are inadequately known and separation of larvae in mixed samples is difficult. Gorbunova (1964) described a number of larval series which she labeled *H. hemilepidotus*, *H. gilberti*, *H. gilberti zapus*, *H. jordani*, and *H. papilio*,[1] but these descriptions are incomplete as well as incorrect for several species (Peden 1978; Richardson and Washington 1980). Hattori (1964) described a series of *H. gilberti* larvae (7.1-32.5 mm), and Peden (1978) illustrated postlarvae (> 18 mm) of *H. hemilepidotus*, *H. spinosus*, *H. zapus*, and *H. jordani*. Richardson and Washington (1980) described larvae of *H. hemilepidotus* and *H. spinosus*. We here provide the first complete description of *H. zapus* larvae, and include comments on larval occurrence in the eastern Bering Sea. This work supplements and clarifies the work of previous researchers by providing diagnostic characters useful in distinguishing the species.

MATERIALS AND METHODS

Specimens of *H. zapus* used in this study were collected during ichthyoplankton surveys conducted in the Bering Sea by the Northwest and Alaska Fisheries Center between 1977 and 1980. Morphological measurements were made on 57 unstained larvae (6.7-22.0 mm SL) following Matarese et al. (1981), except depth at caudal peduncle which was measured at the point of least depth. Measurements were grouped by 1 mm SL intervals, and the means of the measurements within each interval were plotted as percentage of the mean of standard lengths or head lengths within the interval (Kendall and Vinter 1984). A computer-generated best nonparametric curve, based on all data points, was drawn to illustrate relative growth trends. Counts of meristic structures were made on 13 specimens differentially stained according to Dingerkus and Uhler (1977) following procedures outlined in Matarese et al. (1981). Terminology of head spination generally follows Richardson and Laroche (1979) and Richardson and Washington (1980). Illustrations were made by the junior author with a camera lucida, and all specimens were preserved in either 3% Formalin[2] buffered with sodium borate or 100% glycerin.

Identification of *Hemilepidotus zapus*

We have routinely collected three types of Hemilepidotinae larvae during ichthyoplankton surveys in the eastern Bering Sea (1977-80). According to Peden (1978), four species of adults occur in this area: *Hemilepidotus hemilepidotus*, *H. jordani*, *H. zapus*, and *H. papilio*. Although preflexion larvae of *H. hemilepidotus* and *H. jordani* cannot presently be separated, we can separate the two species at notochord flexion according to differences in external pigment along the posterior body. *Hemilepidotus hemilepidotus* larvae develop pigment above the notochord along the posterior body earlier and in greater density than larvae of *H. jordani* (Fig. 1A, B). Initially, the third series of larvae (< 17.0 mm SL) was misidentified as *H. papilio* (see Waldron and Vinter[3]) based on the presence of urostyle pigment (Gorbunova 1964). With the acquisition of larger specimens, > 17.0 mm SL, the complete series was later identified as *H. zapus* based on a set of characters taken in part from Peden (1978) (Table 1). Gorbunova's (1964) specimen attributed to *H. zapus* lacks pigment on the urostyle; of her two illustrations of *H. papilio* (footnote 1) only the 10.7 mm SL

[1]*Hemilepidotus papilio* (= *Melletes papilio* from Gorbunova (1964)).

[2]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Waldron, K. D., and B. M. Vinter. 1978. Ichthyoplankton of the eastern Bering Sea. Unpubl. manuscr., 77 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

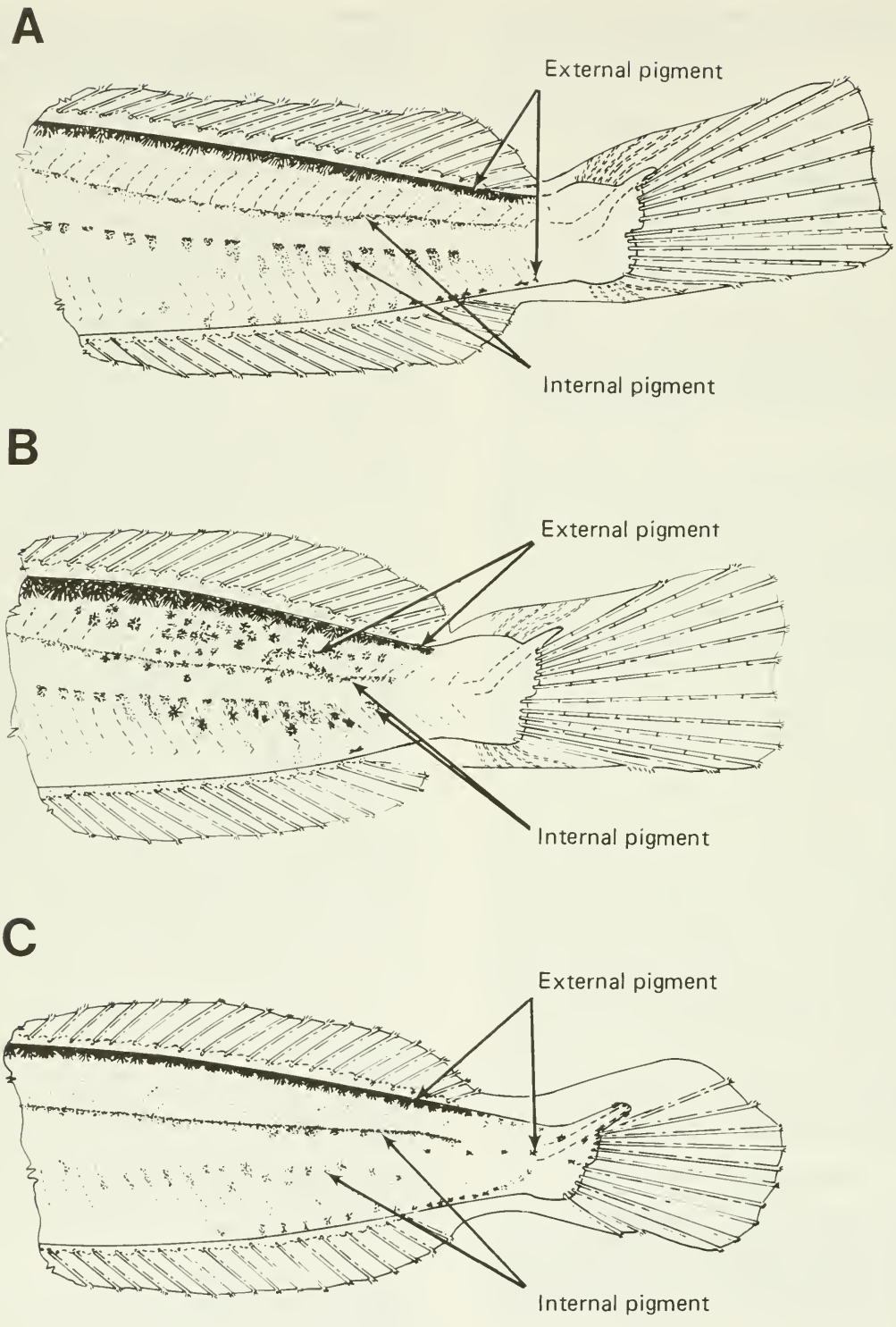

FIGURE 1. – Postanal pigment patterns in *Hemilepidotus* larvae: A) *H. jordani*, 13.7 mm SL; B) *H. hemilepidotus*, 12.7 mm SL; C) *H. zapus*, 12.6 mm SL.

TABLE 1.—Comparison of some important differentiating characters in *Hemilepidotus zapus* and *H. papilio*.

Characters	This study	*H. zapus*[1]	*H. papilio*[1]
Dorsal spines	X-X1	X1 (X1-X11)	X11 (X1-X111)
Pectoral fin rays	16-17	16 (15-17)	17-18 (16-18)
Total soft fin rays; dorsal, anal, and both pectoral fins	71	67-76	69-74
Lateral line pores	54-56	52 (47-58)	59 (49-65)
Number of vertebrae	37-38	37-38	40
Number of horizontal scale rows in ventral band	ca. 8	8 or 9	ca. 4
Dorsal fin notch between third and fourth spine	yes	yes	no

[1]Data are from Peden (1978); mean is followed by range in parentheses.

larvae is *H. zapus*, while the 13.7 mm SL larva lacks urostyle pigment and is probably *H. jordani*.

Early larvae of *H. zapus* (6.5-17.0 mm SL) were linked together by the presence of melanophores above and below the urostyle (Figs. 1C, 2); such melanophores are lacking in all other known Hemilepidotinae larvae. Larvae undergoing notochord flexion can be distinguished from *H. hemilepidotus* by the lack of external pigment along the posterior body and from *H. jordani* by the presence of ventral midline pigment which curves up toward the urostyle (Fig. 1).

After notochord flexion and through the juvenile period, counts of meristic structures as well as a combination of adult characters (Peden 1978) will allow separation of the three species. Postflexion larvae of *H. zapus* have scales on the caudal peduncle that will distinguish them from other, similar-sized Hemilepidotinae larvae. These larvae also have a characteristic notch in the first dorsal fin, between the third and fourth spine, that is present in adults of all *Hemilepidotus* except *H. papilio* (Fig. 2F). A summary of some diagnostic features of all known *Hemilepidotus* larvae is presented in Table 2. Larvae and juveniles of *H. papilio* remain unknown.

General Trends of Development

Pigmentation (Fig. 2)

In the smallest larvae (6-7 mm SL), pigment appears on the head dorsally over the midbrain and on the anterior forebrain. In larger larvae 7-9 mm SL, additional pigment appears at the base of the hindbrain, posterior to the eye and in the opercular area. In postflexion larvae, head pigment increases. Separate pigment patches appear posterior to the eye (usually about 5 or 6 spots) and on the operculum dorsoposterior to the preopercular bone. Larvae 6-7 mm SL have pigment on the nape and on the dorsal surface of the gut. Gut pigment increases laterally with development, and in larger postflexion larvae it becomes more internal than external. By 14-15 mm SL, nape pigment extends ventrally to the dorsal surface of the gut.

There are five general areas of pigmentation in the postanal region: 1) an external row (appearing more or less double) of melanophores along the dorsal midline extending from the nape to the last myomere; 2) a dorsolateral row of internal pigment along the notochord, extending from the nape to about the last 4-7 myomeres; 3) an external row of melanophores along the ventral body midline from midbody (about 11 myomeres after anus) to the last myomere; 4) a ventrolateral row of internal pigment along the notochord, beginning at about 4-6 myomeres after the anus and extending to about 6 or 7 myomeres from the end of the tail; and 5) a few external melanophores along the notochord in the caudal peduncle area, and external melanophores dorsal and ventral to the notochord at the posterior tail tip. Prior to notochord flexion, at about 9.0 mm SL, the anterior ventral midline pigment gradually becomes more internal. In postflexion larvae, this ventral midline row is comprised of < 10 melanophores beginning about 17 myomeres posterior to the anus. By 16.7 mm SL, all the postanal pigment is internal except for the dorsal midline melanophores and a few spots in the caudal peduncle area. After about 17 mm SL, melanophores in the caudal peduncle are no longer visible.

Morphology (Table 3; Fig. 3)

Relative growth trends are summarized in Figure 3. Preanal length, head length, depth at pectoral fin, snout to anal fin length, and snout length increase with development. Eye diameter as a proportion of head length undergoes a gradual decrease with development. Depth at the caudal peduncle and the length from the snout to dorsal fin origin increase sharply with development in larvae about 16.0-19.0 mm SL and then decrease in larger specimens.

Meristic Structures (Tables 4, 5)

Branchiostegal rays have begun to ossify in our smallest specimens (7-8 mm SL), and the adult complement of six rays is completely ossified in larvae $\geq$ 12-13 mm SL.

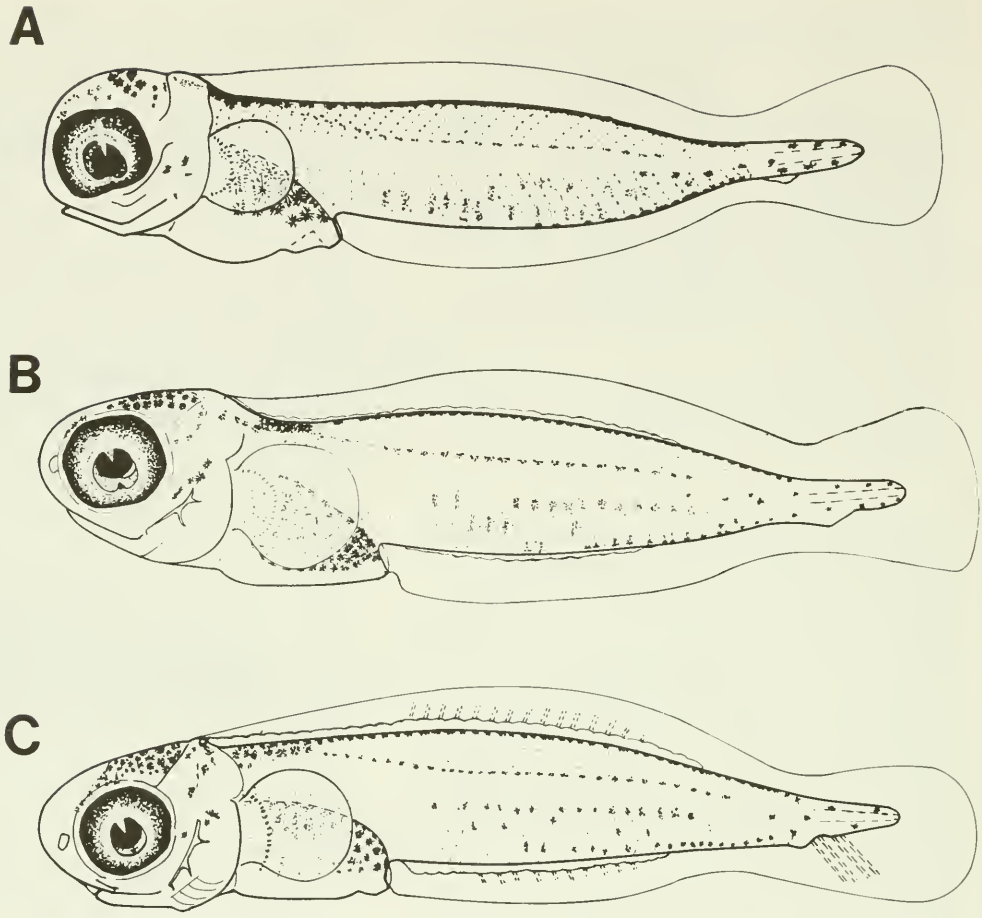

FIGURE 2.–Larvae of *Hemilepidotus zapus*: A) 6.7 mm SL; B) 8.7 mm SL; C) 11.0 mm SL;

Fins–All fin rays show their initial ossification in larvae between 12 and 13 mm SL. Fin formation occurs in the sequence: dorsal spines and fin rays, anal fin rays, and principal caudal fin rays (12-13 mm SL); pectoral fin rays (13-14 mm SL); pelvic spine and fin rays (15-16 mm SL); and secondary caudal fin rays (16-17 mm SL). The pterygiophores supporting dorsal fin rays begin ossifying at 16-17 mm SL, and those supporting anal fin rays begin ossifying at 17-18 mm SL. The largest specimen (20.0 mm SL) has completely ossified dorsal and anal pterygiophores.

Axial skeleton–Neural and haemal spines have started ossification in the smallest larvae 7-8 mm SL, and are fully ossified in larvae 15-16 mm SL. Abdominal vertebral centra are completely ossified in larvae 12-13 mm SL, but the caudal vertebral centra are not fully ossified until larvae are slightly larger at about 14-15 mm SL.

Lateral line scales do not begin ossifying until larvae are 18.0 mm SL, and our largest specimen (20.0 mm SL) has a fully ossified complement of scales.

Spination (Table 5)–The development of head spines is summarized in Table 5. The parietal and nuchal spines fuse in larvae > 13 mm SL and appear as a single spine in the larger larvae 18-20 mm SL. A postocular spine is ossified in larvae 12-13 mm SL but disappears by 18-20 mm SL. A small spine below the eye (infraorbital) ossifies by 14-15 mm SL, but is no longer visible in specimens 20 mm SL.

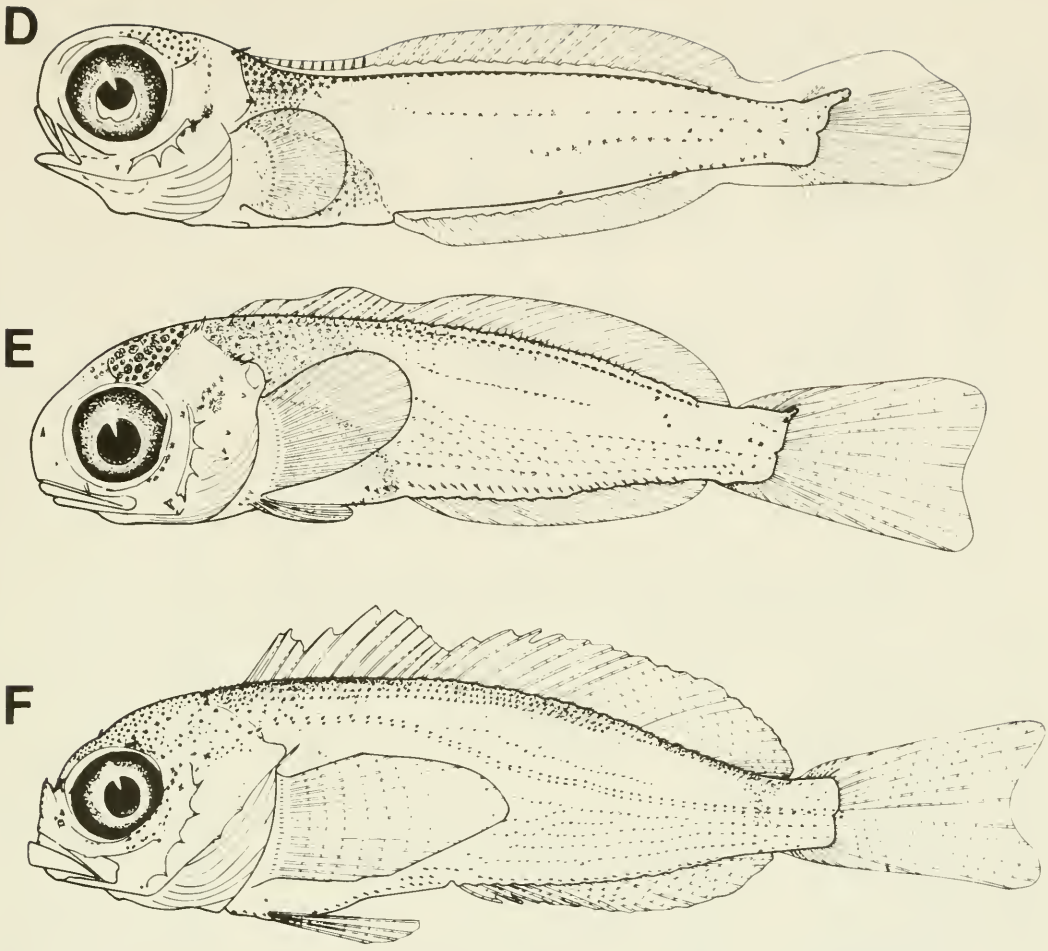

FIGURE 2.—*Continued*—D) 13.0 mm SL; E) 16.7 mm SL; F) 22.8 mm SL.

Occurrence of *Hemilepidotus zapus* in the Eastern Bering Sea

During 8 yr of sampling ichthyoplankton at a total of 250 stations in the eastern Bering Sea (in the approximate area between lat. 60°N and long. 174°W with more intensive sampling between the Pribilof Islands and Unimak Island), only 58 *Hemilepidotus zapus* larvae were collected. The number of positive stations is indicated in Figure 4.

Small *H. zapus* larvae (6.7-10.1 mm SL) were collected during winter in surface water north of the Pribilof Islands (Fig. 4A). Only a single larva (11.0 mm SL) was taken in February 1978 at the surface in about the same area over the slope (Fig. 4A). Our largest collection of larvae (12.2-16.7 mm SL) was made in late April and early May (Fig. 4B). Most of the larvae were collected in neuston nets at stations over the slope, but in May a few larvae were taken over the continental shelf. Larvae primarily occurred south of the Pribilof Islands. The largest larvae (18-22 mm SL) were collected during June and July at scattered stations throughout the area including only one northwest of the Pribilof Islands (Fig. 4C).

Although data are insufficient to document the exact time and geographical extent of spawning, the presence of small larvae indicates some spawning occurs in early winter north of the Pribilof Islands. Peden (1978) indicated that adult and postlarval *H. zapus* have been collected only along the Aleutian Islands. Further studies are needed to investigate whether larvae and juveniles move south to the Aleu-

TABLE 2.—Selected postanal pigmentation characters useful in distinguishing preflexion and flexion *Hemilepidotus* larvae.

Taxon	Pigmentation characters								
	Dorsal midline	Dorso-lateral	Above notochord (internal)	Below notochord (internal)	Ventro-lateral	Ventral midline	Caudal region	Diagnostic	Source
H. spinosus	By 5 mm, a continuous line from head to posteriormost myomere, becoming heavier	By 6 mm, becoming heavier	By 8-9 mm, along length of body	Not obvious	By 6 mm, becoming heavier	From anus to posteriormost myomere, >15 melanophores	Sparse, ventral midline continuous	Lateral, ventral midline	Richardson and Washington 1980
H. hemilepidotus	Until 7 mm unpigmented area between myomeres 4-11, becoming moderately heavy	By 11 mm, moderate	By 6-7 mm, along length of body	By 8-9 mm, begins posterior to anus	By 11 mm, moderate	Begins 9-10 myomeres after anus, <15 melanophores	None	Lateral, lack of caudal pigment	Richardson and Washington 1980, This study
H. jordani[1]	Similar to *H. hemilepidotus* but not as heavy	None	Similar to *H. hemilepidotus*	Similar to *H. hemilepidotus*	Some internal only	By flexion, a few internal melanophores	None	Lack of lateral and caudal pigment	This study
H. zapus	Similar to *H. hemilepidotus* but not as heavy	None	By 6 mm, along length of body	By 8 mm, incomplete, begins posterior to anus	Some internal only	Begins 11 myomeres after anus, <15 melanophores	Ventral midline continues, above and below urostyle	Urostyle	This study
H. gilberti	Pigment begins 8-9 myomeres after anus	None	None[2]	None[2]	None	Begins 10 myomeres after anus, <15 melanophores	None	Unpigmented area along dorsal midline, lack of lateral pigment	Hattori 1964

[1]Preflexion larvae of *H. hemilepidotus* and *H. jordani* cannot presently be separated.
[2]No internal pigment is shown on Hattori's figures.

TABLE 3.—Morphometrics (in millimeters) of larvae and juveniles of *Hemilepidotus zapus*. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Total length	Preanal length	Head length	Snout length	Eye diameter	Depth at pectoral fin	Depth at caudal peduncle	Snout to dorsal	Snout to anal fin
6.5	6.9	2.4	1.3	0.1	0.8	1.3			
6.7	7.4	2.4	1.3	0.1	0.8	1.3			
6.7	7.2	2.4	1.3	0.1	0.8	1.3			
7.1	7.5	2.7	1.4	0.1	0.8	1.3			
7.1	7.7	2.8	1.3	0.1	0.9	1.3			
7.3	7.8	2.7	1.4	0.1	0.9	1.4			
7.6	8.2	2.7	1.3	0.1	0.9	1.4			
7.7	8.3	2.7	1.3	0.1	0.9	1.5			
8.2	8.9	3.1	1.7	0.2	1.0	1.5			
8.2	8.9	3.2	1.8	0.2	1.0	1.6			
8.5	9.1	3.3	1.9	0.3	1.0	1.6			
8.7	9.5	3.5	2.0	0.3	1.1	1.7			
8.7	9.4	3.4	2.0	0.3	1.1	1.7			
9.1	9.8	3.6	1.9	0.3	1.0	1.7			
9.2	10.0	3.6	2.1	0.2	1.1	1.7			
9.2	9.8	3.6	1.9	0.2	1.1	1.7			
9.3	10.1	3.9	2.1	0.2	1.1	1.7			
9.5	10.1	4.0	2.1	0.3	1.2	1.8			
9.8	10.5	3.6	1.9	0.2	1.1	1.7			
10.1	10.9	4.0	2.3	0.3	1.2	1.8			
11.0	12.0	4.4	2.6	0.3	1.3	2.1			
12.0	13.5	5.5	3.2	0.6	1.4	2.5	1.0	3.0	5.8
12.2	14.3	5.5	3.3	0.5	1.5	2.5	0.9		5.8
12.2	14.0	5.6	3.4	0.5	1.5	2.6	0.9	3.3	5.9
12.3	14.4	5.6	3.3	0.4	1.5	2.6	1.0	3.2	5.9
12.6	14.5	5.8	3.3	0.5	1.5	2.8	1.1	3.3	6.0
12.9	15.0	5.7	3.5	0.6	1.5	2.7	1.1	3.3	6.1
12.9	14.6	5.6	3.4	0.4	1.5	2.6	1.0	3.4	6.0
13.0	15.0	5.6	3.7	0.6	1.5	2.6	1.1	3.3	6.0
13.0	15.2	5.6	3.5	0.6	1.6	2.7	1.1	3.3	6.0
13.2	15.4	5.5	3.5	0.6	1.6	2.9	1.1	3.4	5.9
13.5	16.0	6.0	3.5	0.6	1.6	2.8	1.2	3.5	6.4
13.6	16.0	5.9	3.7	0.6	1.5	2.8	1.2	3.3	6.3
13.8	16.1	5.9	3.7	0.6	1.7	3.0	1.2	3.4	6.3
14.0	16.7	6.3	3.7	0.6	1.8	3.2	1.3	3.7	6.6
14.3	17.1	6.5	3.9	0.6	1.8	3.1	1.3	3.7	6.9
14.4	17.2	6.8	4.0	0.6	1.9	3.2	1.4	4.0	7.1
14.5	17.2	6.9	4.0	0.7	1.9	3.3	1.4	4.1	7.2
14.7	17.5	6.8	3.9	0.6	1.9	3.2	1.3	3.8	7.1
14.9	17.9	7.0	4.0	0.6	1.8	3.3	1.4	4.0	7.2
14.9	18.0	7.0	4.1	0.6	2.0	3.4	1.5	4.2	7.3
15.1	18.6	7.2	4.3	0.7	2.0	3.7	1.6	4.2	7.5
15.2	18.3	7.2	4.5	0.7	2.1	3.7	1.6	4.2	7.5
15.3	19.0	7.5	4.7	0.8	2.0	3.9	1.6	4.4	7.8
15.5	19.0	7.3	4.5	0.8	2.0	3.8	1.6	4.5	7.6
15.6	19.0	7.4	4.6	0.7	2.0	3.8	1.6	4.3	7.7
15.9	19.7	7.8	4.7	0.8	2.1	3.9	1.7	4.6	8.1
16.7	20.7	7.9	5.1	0.8	2.1	4.3	1.8	4.8	8.2
16.8	21.3	8.1	5.4	0.8	2.3	4.5	1.7	5.1	8.5
16.9	20.9	8.2	5.2	0.8	2.2	4.4	1.7	5.0	8.6
18.0	23.0	9.0	6.2	1.0	2.3	5.5	1.9	5.2	9.3
19.1	25.0	9.8	6.3	1.0	2.3	5.6	2.0	5.4	10.0
19.3	24.9	10.1	7.0	1.3	2.6	5.7	1.9	6.1	10.5
20.5	26.0	10.5	6.7	1.3	2.5	6.2	2.0	5.5	10.9
21.0	26.5	10.9	7.0	1.3	2.5	6.3	2.1	5.7	11.1
21.0	26.6	11.1	7.0	1.5	2.5	6.3	2.0	6.0	11.5
21.2	27.0	11.4	7.2	1.6	2.5	6.5	2.0	6.1	11.6
22.0	27.5	11.5	7.3	1.3	2.6	6.7	2.1	6.0	11.9

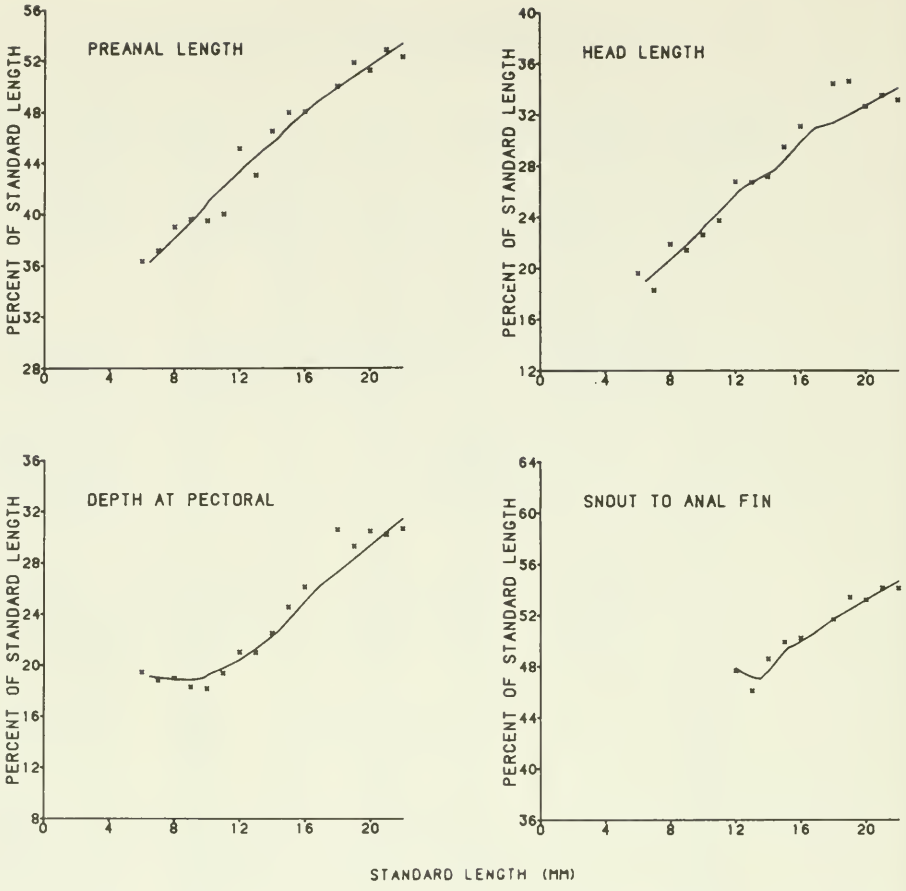

FIGURE 3.–Relative trends in selected morphometric features

TABLE 4.—Development of meristic characters in larvae of *Hemilepidotus*

Size interval (mm SL)	Sample size	Fin rays						
		Dorsal	Anal	Pectoral	Pelvic	Caudal: Principal	Caudal: Secondary	Caudal: Total
7-8	2							
8-9	3							
9-10	2							
[1]10-12	—							
12-13	3	X,11-21	17	8-10	I,0	12	3-5	15-17
13-14	1	XI,21	17	16	I,3	12	9	21
14-15	3	X-XI-20-21	17	13-16	I,3	12	9	21
15-16	2	X,21	17	16	I,4	12	11-13	23-25
16-17	1	XI,20	17	17	I,4	12	15	27
18	1	XI,20	16	16	I,4	12	15	27
20	1	XI,21	17	16	I,4	12	14	26

[1]Specimens in this size group did not accept alizarin stain.
[2]Haemal spines 23-24 are fused.

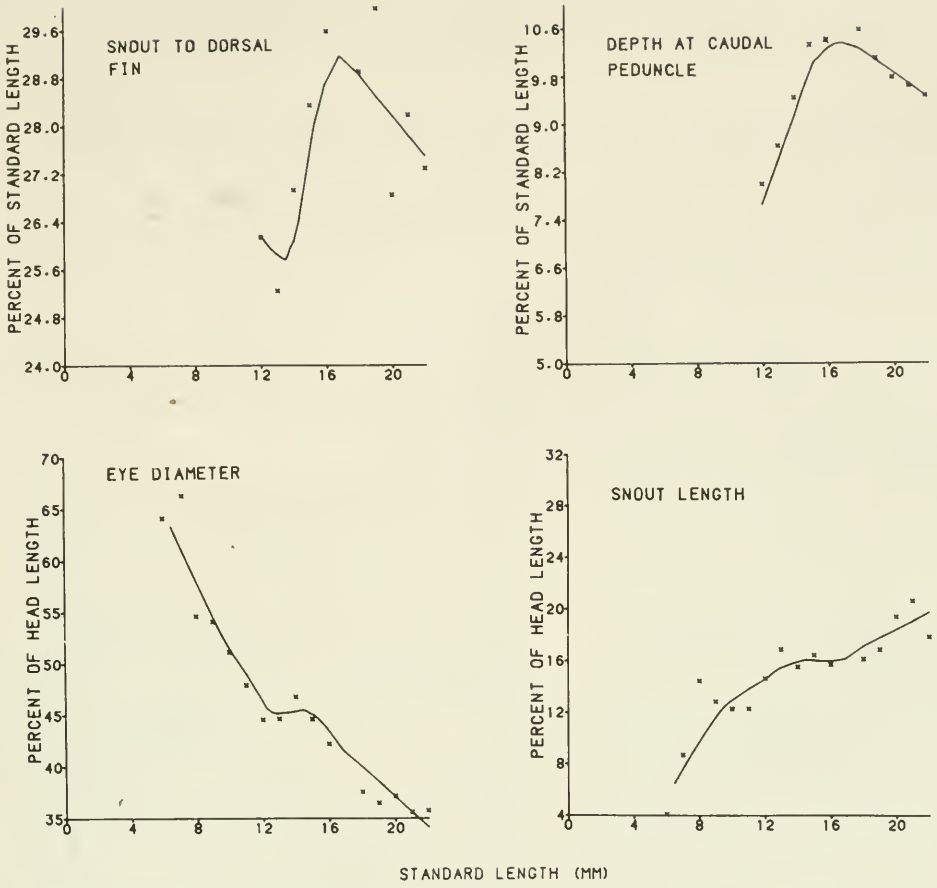

FIGURE 3.—*Continued*—during ontogeny in *Hemilepidotus zapus*.

zapus. Specimens below the dashed line have completed notochord flexion.

Size interval (mm SL)	Sample size	Pterygiophores		Axial skeleton				Branchiostegal rays	Lateral line scales
				Spines		Centra			
		Dorsal	Anal	Neural	Haemal	Precaudal	Caudal		
7-8	2			12-19	9			2-3	
8-9	3			20	10			4	
9-10	2			29	17			5	
[1]10-12	—								
12-13	3			35	22	12	23	6	
13-14	1			36	23	12	25	6	
14-15	3			36	24	12	24-26	6	
15-16	2			37	[2]25	12	26	6	
16-17	1	15		37	24	12	25	6	
18	1	30	16	37	25	12	26	6	54
20	1	31	17	37	24	12	26	6	56

TABLE 5.—Development of spines in the head region of *Hemilepidotus zapus* larvae. Specimens below the dashed line have completed notochord flexion.

Size interval (mm SL)	Sample size	Parietal	Nuchal	Preopercular	Opercular	Postocular	Superior infraorbital	Nasal	Articular	Cleithral	Posttemporal supracleithral
7-8	2	0-1		2							
8-9	3	1		3							
9-10	2	1		3							
[1]10-12											
12-13	3	[2]1	[2]1	4		1			1		1-2
13-14	1	[2]1	[2]1	4		1		1	1		2
14-15	3	[2]1	[2]1	4	3	1	1	1	1		2
15-16	2	[2]1	[2]1	4	3	1	1	1	1		[3]3
16-17	1	[2]1	[2]1	4	3	1	1	1	1	1	[3]3
18	1		1	4	3	0	1	1	1	1	[3]3
20	1		1	4	3	0	0	1	[3]1	1	[3]3

[1]Specimens in this size group did not accept alizarin stain.
[2]Spines are beginning to fuse at base but points can still be observed.
[3]Spine(s) reduced in size.

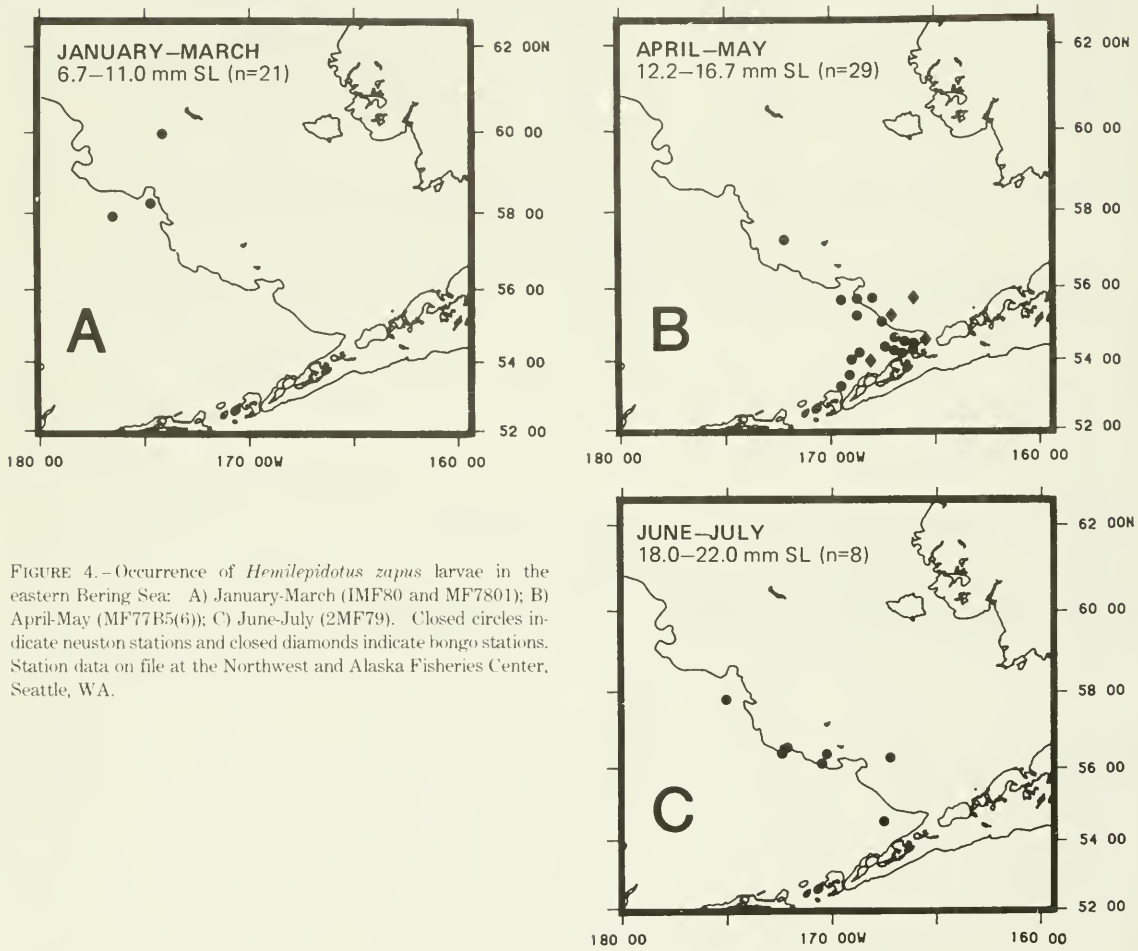

FIGURE 4.—Occurrence of *Hemilepidotus zapus* larvae in the eastern Bering Sea: A) January-March (IMF80 and MF7801); B) April-May (MF77B5(6)); C) June-July (2MF79). Closed circles indicate neuston stations and closed diamonds indicate bongo stations. Station data on file at the Northwest and Alaska Fisheries Center, Seattle, WA.

tians or whether adult *H. zapus* range further north.

Acknowledgments

We thank Jean R. Dunn and Arthur W. Kendall, Jr. (Northwest and Alaska Fisheries Center) for helpful discussions and review of the manuscript. Alex E. Peden (British Columbia Provincial Museum) kindly assisted in the identification of *Hemilepidotus zapus* postflexion larvae.

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ANN C. MATARESE
BEVERLY M. VINTER

NOAA, National Marine Fisheries Service
Northwest and Alaska Fisheries Center
2725 Montlake Boulevard East
Seattle, WA 98112-2097

AN APPROACH TO ESTIMATING AN ECOSYSTEM BOX MODEL

Recent trends in ecosystem modeling have produced complex simulation models which are very data intensive (Andersen and Ursin 1977; Laevastu and Larkins 1981). However, in many situations the construction of a biomass budget for a box model of an ecosystem is relatively simple and can provide important information about the ecosystem standing stock and energy flow (Walsh 1981; Pauly 1982; Polovina 1984).

The ECOPATH model is an analytical procedure to estimate a biomass budget for a box model of an ecosystem given inputs which specify the components of the ecosystem, together with their mortality, diet, and energetics value. A computer program for ECOPATH has been written in BASIC-80, version 5.21, by Microsoft[1] (CP/M version). A listing of the ECOPATH computer program and a user's manual are available from the author.

The ECOPATH model produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the user specified species-groups. The species-groups represent aggregations of species with similar diet and life history characteristics and which have a common physical habitat. The ECOPATH model is not a simulation model with a time component as are some more complex ecosystem models. It estimates a biomass budget for the marine ecosystem in a static situation under the assumption that the ecosystem is at equilibrium conditions.

Equilibrium conditions are defined to exist when the mean annual biomass for each species-group does not change from year to year. This condition results in a system of biomass budget equations which, for species-group i, can be expressed as

> Production of biomass for species i – all predation on species i – nonpredatory biomass mortality for species i – fishery catch for species i = 0 for all i. (1)

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses (B_i's) so the resulting biomass budget equations become a system of simultaneous equations linear in the B_i's. The mean annual biomass estimates are obtained by solving the system of simultaneous linear equations.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The formulation of each term of the biomass budget equation will now be presented in detail.

The Model

Biomass Production

Production (P) for a cohort of animals over 1 yr is defined as

$$P = \int_0^1 N_t \frac{d}{dt}(w_t)\, dt$$

and mean annual biomass (B) for the cohort is defined as

$$B = \int_0^1 N_t\, w_t\, dt$$

where N_t is the number of animals and w_t the mean individual weight at time t.

Allen (1971) investigated the production to biomass (P/B) ratio for a cohort over a range of mortality and growth functions. For a number of growth and mortality functions, including negative exponential mortality and von Bertalanffy growth, the ratio of annual production to mean biomass for a cohort is the annual instantaneous total mortality (Z_i). For a species-group which consists of n cohorts or species, with instantaneous annual total mortality (Z_i) for cohort or species i, where mortality is determined by a negative exponential function and growth by a von Bertalanffy growth function, the total species-group production (P) is the sum of the cohort production (P_i) and can be expresed as

$$P = \sum_{i=1}^{n} P_i = \sum_{i=1}^{n} Z_i B_i. \qquad (2)$$

Under the assumption that the Z_i's are all equal to say Z, then total species-group production can be expressed as

$$P = Z \cdot B$$

where B is the mean annual species-group biomass.

Allen (1971) has also shown that when growth in weight is linear, the P/B ratio is equal to the reciprocal of the mean age for a range of mortality functions. For a number of other growth and mortality functions the ratio of cohort P/B can be the reciprocal of the mean lifespan. Thus, for a range of growth and mortality functions, total species-group production can be expressed as

$$P = C \cdot B$$

where B is the mean annual species-group biomass, and C is a parameter.

In an application of ECOPATH to an ecosystem of French Frigate Shoals where there was very little fishing mortality, the P/B ratio for fishes and crustaceans was taken as the annual instantaneous natural mortality (M); whereas, for primary and secondary producers whose growth is more likely to be linear than the von Bertalanffy, the P/B ratio was estimated as the reciprocal of the mean age (Polovina 1984).

Predation Mortality

The predation mortality is the fraction of the biomass of a species-group which is consumed by all predators excluding fishing mortality. Two types of information are needed. First the food web or predator-prey relationships must be defined. A diet composition matrix DC_{ij} must be specified where an entry DC_{ij} from this matrix refers to the proportion (by weight) of prey j in the diet of predator i. The primary source of this information is the analysis of stomach contents data. At least in one study it has been shown that there is a high correlation between diet indices based on weight, volume, and percentage of occurrence for stomach content data, and thus either index may be used to generate the DC matrix (Macdonald and Green 1983). The second type of information needed to ascertain predation mortality is the food requirements of the predator. The ECOPATH model requires the user to specify FR_i, the ratio of annual consumption to mean annual biomass. The annual food required by the predator is the product of FR_i and B_i.

Some values of daily food required as a fraction of body weight range from 0.005 to 0.02 (Laevastu and Larkins 1981). Based on these daily estimates a range of annual food required as a fraction of mean biomass (FR_i) is 1.8 to 7.3.

Nonpredation Mortality

All mortality attributable to causes other than predation and fishing is termed nonpredatory mortality. The ECOPATH model defines ecotrophic efficiency e_i as the fraction of total production which is removed by fishing and predation mortality. This

was 0.95 in the French Frigate Shoals model. The nonpredator mortality rate is $(1 - e_i) \cdot Z_i$, and the amount of production which goes to nonpredation mortality is

$$(1 - e_i) P_i = (1 - e_i) C_i B_i.$$

For n species-groups the biomass budget Equation (1) becomes a system of n simultaneous equations as follows:

$$C_1 B_1 - \sum_{k=1}^{n} (FR_k) B_k DC_{k1} - (1 - e_1) C_1 B_1 = \text{catch}_1,$$

$$\vdots$$

$$C_i B_i - \sum_{k=1} (\text{FR}_k) B_k DC_{ki} - (1 - e_i) C_i B_i = \text{catch}_i,$$

$$\vdots$$

$$C_n B_n - \sum_{k=1}^{n} (FR_k) B_k DC_{kn} - (1 - e_n) C_n B_n = \text{catch}_n.$$

With input estimates for parameters C_i, FR_i, DC_{ij}, and e_i for all i and j, and catches (catch_i) if there is fishing, this system of equations is a system of n simultaneous equations linear in the unknown B_i's. This system of equations can be expressed in matrix form as $AB = C$, where A is an $n \times n$ matrix of coefficients, B is an n-dimensional vector of mean annual species group biomass, and C is the vector of fishery catch where the ith element is the total catch of the ith species-group.

If the matrix A is of full rank and if there are some fishery catches for some species so the vector C is not null, then there typically exists a unique nontrivial solution vector of biomass B. If there are no fishery catches then it is necessary to provide an estimate of at least one of the mean species group biomass B_i before there exists a unique nontrivial biomass vector B which solves the budget equation. In the application of ECOPATH to an ecosystem at French Frigate Schoals where there was no fishing mortality, the biomasses of three apex predators were estimated from field censuses and treated as known inputs. In this application the ith element of C vector was the annual predation by the three apex predators on the ith species-group.

Five years of field work targeting most of the components of the marine ecosystem at French Frigate Schoals in the Northwestern Hawaiian Islands provided the estimates for many of the input parameters required by the ECOPATH model as well as some estimates of biomass and production to serve to evaluate the estimates produced by the model. The estimates of biomass and production generated by the application of ECOPATH to French Frigate Shoals are given in Figure 1. In general the model's estimates of biomass and production are in good agreement with the available field data (Polovina 1984). In the application of the French Frigate Shoals, the biomasses of the top level carnivores are treated as fixed inputs thus a particularly appropriate validation of the model is the comparison of the estimate of net benthic primary production with an independent estimate from field data. The model estimated net benthic primary production, adjusted to the total 1,200 km^2 habitat of French Frigate Shoals, at 2.3×10^6 kg $\cdot$ $km^{-2} \cdot yr^{-1}$ while the estimate based on field data was 2.5×10^6 kg $\cdot$ $km^{-2} \cdot yr^{-1}$ (Grigg et al. 1984).

The Computer Program

The ECOPATH model has been implemented via two BASIC language programs. The "dialect" of the language used is BASIC-80, version 5.21, by Microsoft (CP/M version). These programs are designed to be used interactively on a terminal or a hard-copy printer. The first program is the input parameter program which accepts the input parameters and formats them into a BASIC sequential file. The second program is the ECOPATH model itself.

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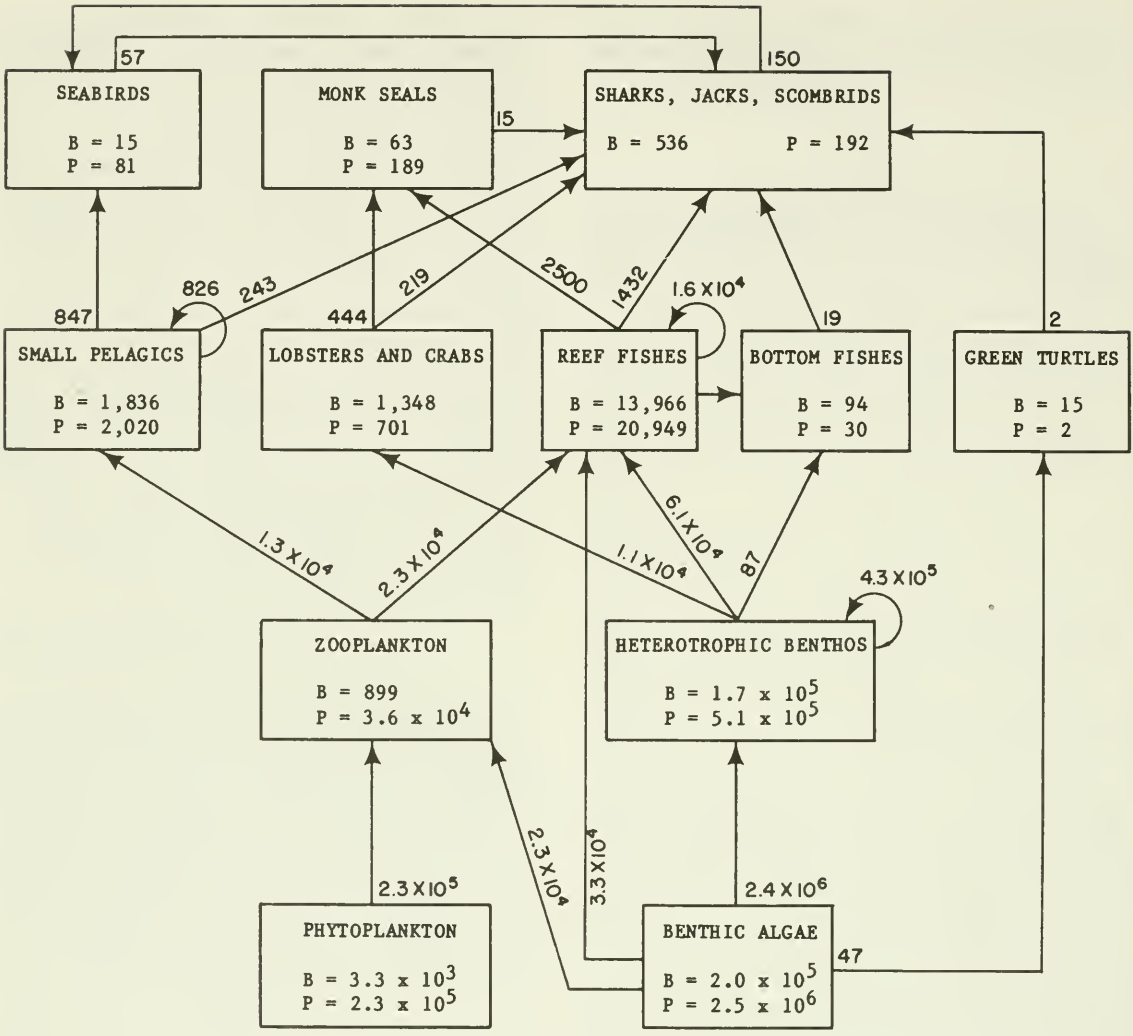

FIGURE 1.—Biomass budget schematic for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of $(kg/km)^2$ based on a habitat area of 1,200 km^2. The values associated with the arrows represent the production from the lower trophic level consumed by the higher trophic level (Polovina in press).

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JEFFREY J. POLOVINA
MARK D. OW

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 3830
Honolulu, HI 96812

FOOD AND FEEDING OF THE TOMTATE, *HAEMULON AUROLINEATUM* (PISCES, HAEMULIDAE), IN THE SOUTH ATLANTIC BIGHT[1]

The tomtate, *Haemulon aurolineatum*, is an abundant demersal fish in a variety of marine habitats in the South Atlantic Bight, the Gulf of Mexico, and the Caribbean Sea (Darcy 1983). They are a reef-associated species (Parrish and Zimmerman 1977), and in the South Atlantic Bight they are most commonly found over hard or "live" bottom reefs in depths < 55 m (Struhsaker 1969; Manooch and Barans 1982; Sedberry and Van Dolah 1984). While occasionally taken in trawl catches over open, sandy habitats on the southeastern continental shelf (Wenner et al. 1980), they are much more abundant in trawls directed at sampling hard bottom, and generally rank in the top three demersal species by number or weight in trawl catches (Wenner 1983; Sedberry and Van Dolah 1984; Sedberry unpubl. data). Although they are frequently caught on hard bottom reefs in the South Atlantic Bight, the dependance of these fishes on hard bottom habitat for food is unknown. Previous investigations in the Caribbean have indicated that tomtate are not obligatory reef dwellers and that they forage extensively in open sandy areas (see Darcy 1983 for review). Because of the importance of this species in the hard bottom ichthyofauna of the South Atlantic Bight and its importance to fisheries associated with hard bottom reefs, a knowledge of its food habits is important to our understanding the ecology of this habitat. Tomtate may be important in transferring energy from the expansive sand areas of the shelf onto the much more restricted hard bottom habitat, and their feeding behavior in the South Atlantic Bight may be important in maintaining the higher biological productivity of hard bottom areas, relative to the open sandy shelf.

To determine foraging habitat of the tomtate, an investigation on food habits was conducted. The purpose of this note is to report the results of that study and to relate the feeding behavior to existing knowledge of the ecology of hard bottom areas in the South Atlantic Bight.

Methods

Tomtate were collected during seasonal cruises in 1980 (two cruises – one in winter and one in summer) and 1981 (four cruises – one each in winter, spring, summer, and fall) by trawl from eight hard bottom reef stations off South Carolina and Georgia. Stations were located in each of three depth zones representing the inner shelf (16-22 m depth, three stations), middle shelf (23-38 m, four stations), and the outer shelf (47-67 m, one station). Detailed descriptions of station locations and habitat can be found in Sedberry and Van Dolah (1984) and Wenner et al. (1984). Each station was mapped using loran C and underwater television, and all sampling was conducted in hard bottom areas mapped by using this technique (Sedberry and Van Dolah 1984).

Tomtate were measured (standard length, SL) at sea and their stomachs removed if not conspicuously empty. Stomachs were individually labeled and preserved in 10% seawater-Formalin[2].

Stomachs were washed in tap water and transferred to 50% isopropanol in the laboratory, and contents of individual stomachs were sorted by taxa and counted. Colonial forms (e.g., hydroids, bryozoans) and algae were counted as one organism. Volume displacement of food items was measured using a graduated cylinder, or estimated by using a 0.1 cm^2 grid (Windell 1971).

Since the methods of food habits quantification are variously biased (Hynes 1950; Pinkas et al. 1971; Windell 1971), the relative contribution of different food items to the total diet was determined using three methods: 1) percent frequency occurrence (F), 2) percent numerical abundance (N), and 3) percent volume displacement (V). These three values were calculated for individual prey species, for prey grouped by higher taxonomic categories, and for higher taxonomic categories pooled for 100 mm intervals of standard length. To determine the dependance of tomtate on hard bottom prey organisms, stomach samples were compared with benthic samples using Ivlev's index of electivity (Ivlev 1961), calculated as follows:

$$E = \frac{P_1 - P_2}{P_1 + P_2}$$

where P_1 is the percentage of the diet comprised by a given prey taxon and P_2 is the percentage of the food complex in the environment (i.e., in benthic samples) comprised by the same prey taxon. Electivity values range from -1 to $+1$. Negative values imply that the prey species is avoided by the predator or that it

[1]Contribution No. 179, South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

is unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species which occur in a different habitat than those sampled by the benthic sampler. A value near zero implies no selectivity by the predator; i.e., the fish is feeding on the prey in proportion to the prey's relative abundance.

Benthic samples and stomach collections were pooled by depth zone (inner, middle, and outer shelf) for comparison; however, too few tomtate for adequate comparison were collected at outer shelf stations. Benthic samples were obtained with diver-operated suction sampler at the seven inner and middle shelf, hard bottom sites during the same time periods in 1980 and 1981 as the fish collections were made. The suction sampler is very effective at sampling macroinvertebrates on hard substrates (Chess 1979; Wenner et al. 1983). Five replicate benthic samples were taken during the six cruises at each reef that was sampled for fishes, and these samples (30 for each reef) are believed to be adquate representatives of the hard bottom invertebrate fauna in

TABLE 1.—Percent frequency occurrence (F), percent number (N), and percent volume (V) of food items in *Haemulon aurolineatum* stomachs collected at hard bottom areas in 1980 and 1981.

Taxon	Food item	F	N	V
Algae				
	Sargassum sp.	1.0	0.1	0.1
Cnidaria				
	Hydrozoa			
	Dynamena cornicina	1.0	0.1	<0.1
	Lictorella convallaria	1.0	0.1	<0.1
	Sertularia sp.	1.0	0.1	<0.1
	Total Hydrozoa	3.2	0.2	<0.1
	Anthozoa			
	Actiniaria undetermined	5.3	0.4	0.6
Platyhelminthes				
	Turbellaria undetermined	5.3	1.0	0.7
Annelida				
	Polychaeta			
	Ampharete sp.	1.0	0.1	<0.1
	Amphinomidae undetermined	1.0	0.1	<0.1
	Arabella iricolor	2.1	0.2	0.5
	Arabellidae undetermined	1.0	0.1	0.1
	Armandia maculata	6.3	2.4	0.3
	Capitellidae undetermined	5.3	0.4	0.4
	Ceratonereis mirabilis	1.0	0.1	<0.1
	Chloeia sp.	1.0	0.1	0.2
	Chloeia viridis	1.0	0.1	0.4
	Chone americana	2.1	0.2	<0.1
	Diopatra cuprea	1.0	0.1	<0.1
	Drilonereis sp.	2.1	0.2	0.1
	Eunice vittata	1.0	0.1	<0.1
	Eunice websteri	1.0	0.1	<0.1
	Eunicidae undetermined	1.0	0.1	<0.1
	Exogone dispar	2.1	0.2	<0.1
	Glycera sp.	5.3	0.4	1.2
	Glycera americana	3.2	0.2	0.8
	Glycera tesselata	2.1	0.2	0.3
	Goniadides carolinae	1.0	0.1	<0.1
	Harmothoe sp.	2.1	0.2	<0.1
	Lumbrinerides acuta	1.0	0.1	<0.1
	Lumbrineris coccinea	2.1	0.2	0.9
	Lumbrineris sp.	1.0	0.1	0.9
	Malanidae undetermined	3.2	0.5	0.2
	Nephtyidae undetermined	1.0	0.1	<0.1
	Nephtys incisa	1.0	0.1	<0.1
	Notomastus americanus	1.0	0.1	<0.1
	Notopygos crinita	1.0	0.1	0.1
	Onuphis sp.	1.0	0.1	<0.1
	Onuphis eremita	1.0	0.1	<0.1
	Onuphis nebulosa	1.0	0.1	0.4
	Opheliidae undetermined	1.0	0.1	<0.1
	Phyllodoce castanea	1.0	0.1	<0.1
	Phyllodoce groenlandica	1.0	0.1	0.1
	Phyllodoce longipes	1.0	0.2	<0.1
	Phyllodoce sp.	1.0	0.1	<0.1
	Phyllodocidae undetermined	1.0	0.1	<0.1
	Polychaeta undetermined	5.3	0.4	3.1
	Progoniada regularis	1.0	0.1	<0.1
	Psalmmolyce ctenidophora	2.1	0.2	1.5
	Sabellidae undetermined	1.0	0.1	0.2
	Scoloplos rubra	1.0	0.1	0.2
	Sphaerodoridae undetermined	1.0	0.1	<0.1
	Syllidae undetermined	2.1	0.2	<0.1
	Syllis sp.	3.2	0.2	0.1
	Syllis regulata carolinae	1.0	0.1	<0.1
	Terebellidae undetermined	2.1	0.2	2.0
	Travisia parva	1.1	0.2	0.1
	Total Polychaeta	46.3	8.7	14.6
Mollusca				
	Gastropoda			
	Caecum pulchellum	1.0	0.1	<0.1
	Diodora cayenensis	1.0	0.1	<0.1
	Gastropoda undetermined	1.0	0.1	0.4
	Naticidae undetermined	1.0	0.1	<0.1
	Total Gastropoda	3.2	0.3	0.5
	Pelecypoda			
	Ervilia concentrica	5.3	38.2	6.3
	Mactra fragilis	1.0	0.1	0.2
	Pelecypoda larvae	1.0	0.1	<0.1
	Total Pelecypoda	7.4	38.3	6.5
	Cephalopoda			
	Octopus sp.	1.0	0.1	0.9
Pycnogonida				
	Anoplodactylus insigniformis	1.0	0.1	<0.1
Crustacea				
	Copepoda			
	Calanopia americana	5.3	13.0	0.3
	Longipedia helgolandica	2.1	0.6	<0.1
	Microsetella norvegica	1.0	0.2	<0.1
	Saphirella tropica	1.0	0.1	<0.1
	Temora stylifera	3.2	0.4	<0.1
	Temora turbinata	6.3	1.2	<0.1
	Undinula vulgaris	1.0	0.1	<0.1
	Total Copepoda	13.7	15.4	0.4
	Stomatopoda			
	Gonodactylus bredini	2.1	0.2	1.4
	Lysiosquilla scabricauda	1.0	0.1	1.7
	Stomatopoda larvae	3.2	0.3	0.3
	Stomatopoda undetermined	4.2	0.3	0.4
	Total Stomatopoda	10.5	0.8	3.8
	Mysidacea			
	Bowmaniella portoricensis	3.2	0.2	0.1
	Cumacea			
	Cumacea B	1.0	0.1	<0.1
	Oxyurostylis smithi	3.2	0.2	<0.1
	Total Cumacea	4.2	0.3	<0.1

each depth zone (Wenner et al. 1983, 1984). Details of benthic sampling and structure of the invertebrate communities are described elsewhere (Wenner et al. 1983, 1984). The electivity index was calculated for each species that were numerically dominant in fish stomachs or in benthic samples collected within the two depth zones (inner and middle shelf).

Results and Discussion

Haemulon aurolineatum had a generalized diet and fed on about 120 species of prey (Table 1). Polychaetes and amphipods were the most important food and were eaten with almost the same frequency. Polychaetes, however, made up a large volume of prey because of their large size. Decapods were also frequently consumed, but made up a small percentage of the volume or number of prey items. Pelecypods were the most abundant prey and cephalochordates, while infrequently consumed, made up a large portion of food volume because of their large size. Fishes also made up a large portion of food volume and copepods, though small in volume displacement, were often eaten in large numbers.

TABLE 1.—*Continued.*

Taxon Food item	F	N	V
Tanaidacea			
Apseudes sp. B	1.0	0.7	<0.1
Isopoda			
Carpias bermudensis	1.0	0.1	<0.1
Erichsonella filiformis	1.0	0.1	<0.1
Eurydice littoralis	3.2	0.2	0.1
Paracerceis caudata	1.0	0.1	<0.1
Total Isopoda	6.3	0.4	0.1
Amphipoda			
Acanthonotozomatidae	1.0	0.1	<0.1
Ampelisca sp.	1.0	0.1	<0.1
Ampelisca cristoides	1.0	0.1	0.1
Ampelisca schellenbergi	3.2	0.3	0.1
Ampelisca vadorum	1.0	0.1	0.1
Amphipoda E	3.1	0.2	<0.1
Amphipoda G	1.0	0.2	<0.1
Amphipoda undetermined	2.1	0.2	0.1
Caprella equilibra	13.7	1.7	0.2
Caprella penantis	3.2	0.4	0.1
Cerapus tubularis	1.0	0.1	<0.1
Elasmopus sp. A	2.1	0.4	<0.1
Elasmopus sp.	1.0	0.1	<0.1
Erichthonius brasiliensis	12.6	2.1	0.2
Gammaropsis sp.	2.1	0.4	<0.1
Lembos unicornis	1.0	0.1	<0.1
Leucothoe spinicarpa	1.0	0.1	<0.1
Liljeborgia sp. A	2.1	0.2	<0.1
Luconacia incerta	2.1	1.5	0.1
Lysianopsis alba	4.2	0.7	0.1
Melita appendiculata	2.1	1.0	0.1
Metharpinia floridana	1.0	0.2	<0.1
Microjassa sp. A	1.0	0.2	<0.1
Monoculodes sp.	1.0	0.1	<0.1
Photis sp.	3.1	0.4	<0.1
Photis pugnator	1.0	0.2	<0.1
Phtisica marina	2.1	0.3	<0.1
Rhepoxynius epistomus	2.1	0.2	<0.1
Rudilemboides naglei	6.3	0.7	<0.1
Stenopleustes sp. A	1.0	0.1	<0.1
Stenothoe sp.	3.2	0.2	<0.1
Stenothoe georgiana	5.3	0.8	<0.1
Synchelidium americanum	1.0	0.1	<0.1
Tiron tropakis	1.0	0.1	<0.1
Total Amphipoda	47.4	12.8	1.3
Decapoda			
Albunea paretii zoea	1.0	0.1	<0.1
Alpheus normani	1.0	0.1	<0.1
Brachyura megalopae	1.0	1.2	0.1
Brachyura undetermined	2.1	0.2	0.3
Callianassa atlantica	1.0	0.1	0.9
Decapoda larvae	1.0	0.1	<0.1
Leptochela sp.	1.0	0.1	0.4
Leptochela papulata	7.4	0.7	1.7
Lucifer faxoni	3.2	0.4	<0.1
Lysmata sp.	1.0	0.2	<0.1
Natantia undetermined	4.2	0.4	0.6
Neopontonides beaufortensis	1.0	0.1	<0.1
Paguridae	1.0	0.1	<0.1
Periclimenaeus schmitti	1.0	0.1	<0.1
Periclimenes sp.	1.0	0.1	0.1
Periclimenes longicaudatus	2.1	0.2	0.1
Processa sp.	4.2	0.3	0.9
Processa hemphilli	1.0	0.1	0.2
Synalpheus minus	1.0	0.1	0.1
Synalpheus townsendi	1.0	0.1	<0.1
Thor sp.	1.0	0.1	0.2
Thor floridanus	1.0	0.1	<0.1
Trachypenaeus constrictus	2.1	0.2	0.1
Xanthidae	1.0	0.1	0.2
Total Decapoda	33.7	4.9	6.2
Sipunculida			
Sipunculida D	1.0	0.1	<0.1
Bryozoa			
Amathia distans	1.0	0.1	<0.1
Crisia sp.	1.0	0.1	<0.1
Diaperoecia floridana	2.1	0.2	<0.1
Discoporella umbellata	1.0	0.1	<0.1
Total Bryozoa	5.3	0.4	0.1
Echinodermata			
Echinoidea			
Clypeasteroidea undetermined	1.0	0.7	<0.1
Ophiuroidea			
Hemipholis elongata	1.0	0.1	<0.1
Ophiothrix angulata	3.2	0.4	0.4
Ophiuroidea undetermined	17.9	1.5	1.5
Total Ophiuroidea	22.1	1.9	1.9
Chaetognatha			
Chaetognatha undetermined	1.0	0.1	<0.1
Chordata			
Cephalochordata			
Branchiostoma caribaeum	4.2	12.4	41.6
Pisces			
Bothidae undetermined	1.0	0.1	0.2
Clupeidae undetermined	1.0	0.1	1.0
Hypleurochilus geminatus	1.0	0.1	0.4
Teleostei larvae	1.0	0.1	<0.1
Teleostei undetermined	10.5	0.7	18.8
Total Pisces	14.7	1.0	20.5
Number of stomachs examined:	154		
Examined stomachs with food:	95		

Ophiuroids were frequently consumed but were usually represented in stomachs by small arm fragments.

Small (1-100 mm SL) tomtate had a diet dominated numerically by very small crustaceans (copepods) and volumetrically by fishes and decapods (Table 2). Amphipods were most abundant prey taxon for 101-150 mm tomtate and polychaetes made up the greatest volume of food. Large (151-200 mm SL) tomtate primarily consumed pelecypods, which were the most abundant taxon, and cephalochordates, which were abundant in the diet and made up the greatest prey volume.

Many hard bottom invertebrates that were abundant in suction samples at inner and middle shelf sites were not important in the diet of tomtate (Table 3). Of the eight dominant hard bottom invertebrate species, only two (the polychaete *Chone americana* and the corophoid amphipod *Erichthonius brasiliensis*) at inner shelf sites and one (the caprellid amphipod *Luconacia incerta*) at middle shelf sites made up a greater percentage of the diet than they did of benthic samples. On the other hand, invertebrates that were common in stomachs were generally not abundant in benthic samples and electivity values were usually positive.

Tomtate are apparently not completely dependent on hard bottom habitat for prey. Some of the most abundant prey species are pelagic (e.g., brachyuran megalopae, copepods). Most benthic prey are infaunal species that are restricted to soft sediments. *Armandia maculata*, a dominant prey species on the inner shelf, is a deposit-feeding polychaete that burrows in soft sediments (Fauchald and Jumars 1979). *Ervilia concentrica*, an important prey species on the middle shelf, was not collected at any of the 11 hard bottom stations. This bivalve is common in soft sediments (Porter 1974). The cephalochordate *Branchiostoma caribaeum*, a common prey species on the middle shelf that was very rare in benthic samples, is also an infaunal sand bottom species (Hildebrand and Schroeder 1928). Thus, a large portion of the prey of *Haemulon aurolineatum* are not hard bottom epifaunal species, suggesting that tomtate are not

TABLE 2.—Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Haemulon aurolineatum*, by length interval.

	Length Intervals (mm SL)								
	1-100			101-150			151-200		
Prey taxon	F	N	V	F	N	V	F	N	V
Algae	4.8	0.4	2.6						
Cnidaria									
Hydrozoa							6.2	0.3	<0.1
Anthozoa				8.3	1.1	3.0	6.3	0.3	0.4
Turbellaria				12.5	4.0	6.3	4.2	0.7	0.1
Annelida	19.0	1.5	11.4	62.5	15.6	35.9	50.0	9.4	13.5
Mollusca									
Gastropoda				8.3	1.1	4.7	2.1	0.2	<0.1
Pelecypoda				4.1	0.6	<0.1	12.5	57.2	8.0
Cephalopoda							2.1	0.1	1.1
Arthropoda									
Pycnogonida				4.2	0.6	0.1			
Copepoda	47.6	77.1	14.4	4.2	0.6	<0.1	4.2	0.3	<0.1
Stomatopoda	19.0	1.9	14.7	12.5	1.7	2.2	6.2	0.3	4.0
Mysidacea							6.2	0.3	0.1
Cumacea	4.8	0.4	0.2				6.2	0.3	<0.1
Tanaidacea				4.2	0.6	<0.1			
Isopoda				12.5	1.7	0.1	6.2	0.3	0.2
Amphipoda	33.3	6.0	7.3	79.2	58.3	7.7	39.6	5.9	0.5
Decapoda	19.0	9.8	20.8	33.3	5.6	11.3	39.6	3.2	5.6
Sipunculida	4.8	0.4	0.7						
Bryozoa				8.3	1.1	0.4	6.2	0.3	<0.1
Echinodermata									
Echinoidea							2.1	0.1	<0.1
Ophiuroidea	14.3	1.1	1.7	25.0	5.0	8.0	22.9	1.4	1.0
Chaetognatha	4.8	0.4	0.4						
Chordata									
Cephalochordata				4.2	0.6	2.4	6.2	18.4	51.1
Pisces	4.3	1.1	26.0	16.7	2.2	17.8	12.5	0.7	14.1
Number of stomachs examined:		28			44			79	
Examined stomachs with food:		21			24			48	
Mean length of fish with food (mm SL):		71.5			138.2			168.3	
Length extremes in interval (mm SL):		49-99			101-150			151-198	

restricted to hard bottom habitat for food resources. Although numerous in hard bottom areas (it ranked third in total number and second in total weight in trawl catches over all eight trawlable stations and six sampling periods combined in 1980 and 1981), *Haemulon aurolineatum* has been characterized as a reef-related species; i.e., it uses the reef for only part of each day (Parrish and Zimmerman 1977). Randall (1967) found sand-dwelling organisms in 16 tomtate stomachs he examined, but the habitat of the decapods, the predominant prey, could not be inferred from his results. Parrish and Zimmerman (1977) noted a diet dominated by sand-flat invertebrates for an unspecified number of tomtate collected in the Caribbean. Parrish and Zimmerman (1977) reported nocturnal foraging, with tomtate sheltering in the reef during the day. During extensive (about 70 dives) daytime scuba observations by the author off of South Carolina and Georgia, no tomtate that exhibited foraging behavior was seen, and large schools were often noted "stacked up" at the edge of rock ledges protruding out into sand areas. Apparently, nocturnal feeding behavior described for tomtate in the Caribbean is also typical for the species in the South Atlantic Bight. Tomtate forage, apparently at night, on sand bottom areas of the shelf or in sand patches often found adjacent to rock outcrops, returning to the reefs for shelter during the day. This behavior probably results in considerable energy transfer, in the form of feces, from open sand bottom areas of the shelf onto hard bottom reefs.

The fact that two hard bottom invertebrate species (*Erichthonius brasiliensis* and *Luconacia incerta*) were common in tomtate stomachs and that many additional hard bottom species (e.g., hydroids, many amphipods, alpheid decapods, and bryozoans) are occasionally eaten indicates that tomtate also forage to a limited extent on hard bottom.

The high diversity found in hard bottom invertebrate communities (Wenner et al. 1983) could be attributed, in part, to predation by abundant and diverse fish communities (Petersen 1979). However, as noted by Wenner et al. (1983), available data indicate that few dominant species of hard bottom invertebrates are heavily preyed upon by fishes (Sedberry and Nimmich[3]). Tomtate, an abundant

[3]Sedberry, G. R., and T. A. Nimmich. Food habits of some fishes associated with live bottom habitat off the South Atlantic coast of the U.S.A. Manuscr. in prep. South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412.

TABLE 3.—Relative abundance (percent of total number of individuals) and electivity index values (*E*) of dominant species in suction samples (Group A) and *Haemulon aurolineatum* stomachs (Group B) by depth zone. Dominant species included those that ranked in the five most abundant species within each Group (A or B) in either depth zone, for collections pooled for all years and seasons.

	Percent of total number of individuals					
	Inner shelf			Middle shelf		
	Benthic samples	Fish stomachs	*E*	Benthic samples	Fish stomachs	*E*
Group A:						
Chone americana	0.33	0.36	0.04	0.81	0.09	−0.79
Erichthonius brasiliensis	2.89	9.32	0.53	0.30	0.19	−0.24
Exogone dispar	3.71	0.72	−0.68	0.47		−1.00
Filograna implexa	20.42		−1.00	63.87		−1.00
Luconacia incerta	3.27	0.36	−0.80	1.03	1.77	0.26
Malacoceros glutaeus	0.41		−1.00	0.81		−1.00
Podocerus sp. A	2.87		−1.00	0.27		−1.00
Syllis spongicola	2.15		−1.00	1.90		−1.00
Total	36.05	10.76		69.46	2.05	
Group B:						
Armandia maculata	0.22	10.75	0.96	0.03	0.19	0.73
Brachyura megalopae		6.09	1.00			0.00
Branchiostoma caribaeum			0.00	0.01	15.69	0.99
Calanopia americana		0.36	1.00		16.34	1.00
Caprella equilibra	1.55	2.87	0.30	0.34	1.40	0.61
Erichtonius brasiliensis	2.89	9.32	0.53	0.30	0.19	−0.24
Ervilia concentrica		0.36	1.00		48.18	1.00
Luconacia incerta	3.27	0.36	−0.80	1.03	1.77	0.26
Melita appendiculata	0.43	4.66	0.83	0.27		−1.00
Temora turbinata		4.30	1.00		0.28	1.00
Total	8.36	39.07		1.98	84.04	
Stomachs with food:		43			50	

predator on hard bottom areas (Sedberry and Van Dolah 1984), do not serve as "keystone" predators (Paine 1969) which influence community structure of invertebrates on South Atlantic Bight hard bottom reefs.

Acknowledgments

I thank the many individuals of the South Carolina Marine Resources Center who were involved in all phases of the 3-yr BLM (contracts AA551-CT9-27 and AA551-CT1-18) and MMS (contract 14-12-0001-29185) funded study of hard bottom habitat in the South Atlantic Bight. I especially thank D. M. Knott, R. F. Van Dolah, and E. L. Wenner for providing the data on macrobenthos that was used in the electivity analysis; C. B. O'Rourke and E. C. Roland (polychaetes), H. Porter (bivalves), and E. L. Wenner (decapods) for help in prey identification; C. A. Barans, C. A. Wenner, and the anonymous reviewers for comments that improved the manuscript; and N. M. Beaumont for processing the manuscript.

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George R. Sedberry

South Carolina Marine Resources Research Institute
P.O. Box 12559
Charleston, SC 29412

SEMILUNAR REPRODUCTIVE CYCLES IN *FUNDULUS HETEROCLITUS* (PISCES: CYPRINODONTIDAE) IN AN AREA WITHOUT LUNAR TIDAL CYCLES

Although lunar spawning rhythms are relatively common in species of shallow-water fish, semilunar reproductive cycles have been reported in a small but growing number of species (Korringa 1947; Johannes 1978). Species with the best documented semilunar gonad and spawning cycles include the California grunion, *Leuresthes tenuis*, (Clark 1925); Atlantic silversides, *Menidia menidia*, (Middaugh 1981); the tropical coral reef saddleback wrasse, *Thallassoma duperrey*, (Ross 1983); two tropical damselfishes, *Pomacentrus flavicauda* and *P. wardi*, (Doherty 1983), and gulf killifish, *Fundulus grandis*, (Greeley and MacGregor 1983); and the salt marsh mummichog, *Fundulus heteroclitus*, (Taylor et al. 1979; Taylor and DiMichele 1980). On the east coast of North America, *F. heteroclitus* move up onto marsh surfaces during high spring tides to spawn either in empty mussel (*Geukensia demissa*) shells or in the outer leaves of salt marsh plants (*Spartina alterniflora*) where oxygen levels are relatively high and sedimentation rates are relatively low (Able and Castagna 1975; Taylor et al. 1977; Kneib and Stiven 1978; Taylor and DiMichele 1983). Its eggs are extremely tolerant of desiccation and hatch on the next series of high spring tides. In addition, semilunar rhythms of larval hatching are well known for intertidal chironomid insects (Newmann 1978) and for several species of intertidal and estuarine crabs (see Christy 1982; Forward et al. 1982).

In most cases, the proximal factors (sensu Giese and Pearse 1974) responsible for initiating and synchronizing these semilunar cycles are unknown. However, among the factors postulated as cues are tidal rhythms in water turbulence and hydrostatic pressures (Korringa 1947; Newmann 1978; Weld and Meier 1982; Ross 1983); tidal regimes in the habitat (Forward et al. 1982); photoperiod in combination with tidal fluctuations in water temperature (Miller et al. 1981), in combination with time of high tide (Middaugh 1981; Middaugh and Takita 1983), or in combination with interrupted current velocity (Middaugh and Hemmer 1984); and moonlight (Saigusa 1980). In addition to its wide distribution in coastal marshes with distinct lunar cycles of spring and neap tides, *F. heteroclitus* is abundant in extensive shoreline habitats and marshes of Chesapeake Bay, where tidal ranges are small and changes in water level caused by barometric pressure and wind frequently and unpredictably override lunar tidal levels and obliterate semilunar tidal cycles. In the present study, we measured the reproductive activity of *F. heteroclitus* in an area without lunar tidal cycles in order to determine if semilunar reproductive rhythms occur. The occurrence of semilunar reproductive rhythms would suggest that the proximal cues regulating the reproductive cycles are not factors associated with changes in tidal levels, such as pressure, or turbulence of currents.

Methods

This study was conducted from May through August 1982 at a small tidal creek (Muddy Creek) which flows into the Rhode River (lat. 38°51′N, long. 76°32′W), a subestuary on the western shore of central Chesapeake Bay, located about 11.3 km south of Annapolis, MD. The creek bottom consists of fine clays and silts, and its banks are fringed by a cattail (*Typha angustifolia*) marsh. Water level was measured with a Honeywell[1] diffused silicon differential pressure transmitter (accurate to ± 1.238 cm) at a station operated by the U.S. Geological Survey on the Rhode River near the mouth of Muddy Creek about 1,000 m from the site where fish were sampled. Changes in water level at the monitoring station accurately reflect water levels at the sampling site (D. L. Correll[2] and R. L. Cory[3]). Measured daily high water levels were compared with predicted high tidal levels published for the Rhode River (National Oceanic and Atmospheric Administration 1981).

Fundulus heteroclitus is the most abundant fish in the creek (Hines unpubl. data). Fish were sampled every 2-3 d during the hours of 0730-1230, using unbaited minnow traps set just above low water level. Each sample consisted of 8-12 males and 8-12 females which were tested for readiness to spawn, and another 8-12 of each sex were taken to determine gonad indices. Readiness to spawn was determined in the field by applying gentle pressure from anterior to posterior along the ventral surface of the fish. Release of sperm or eggs was interpreted as the fish being ripe. The gonad index for each fish in the sample was determined by dissecting out the testes or ovaries and by drying the gonad and body to constant weight at 60°C and weighing them to the near-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]D. L. Correll, Assistant Director, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, pers. commun. September 1982.

[3]R. L. Cory, Oceanographer, U.S. Geological Survey, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, pers. commun. September 1982.

est 1×10^{-5} g. The gonad index equals the (gonad weight/body weight) $\times$ 100.

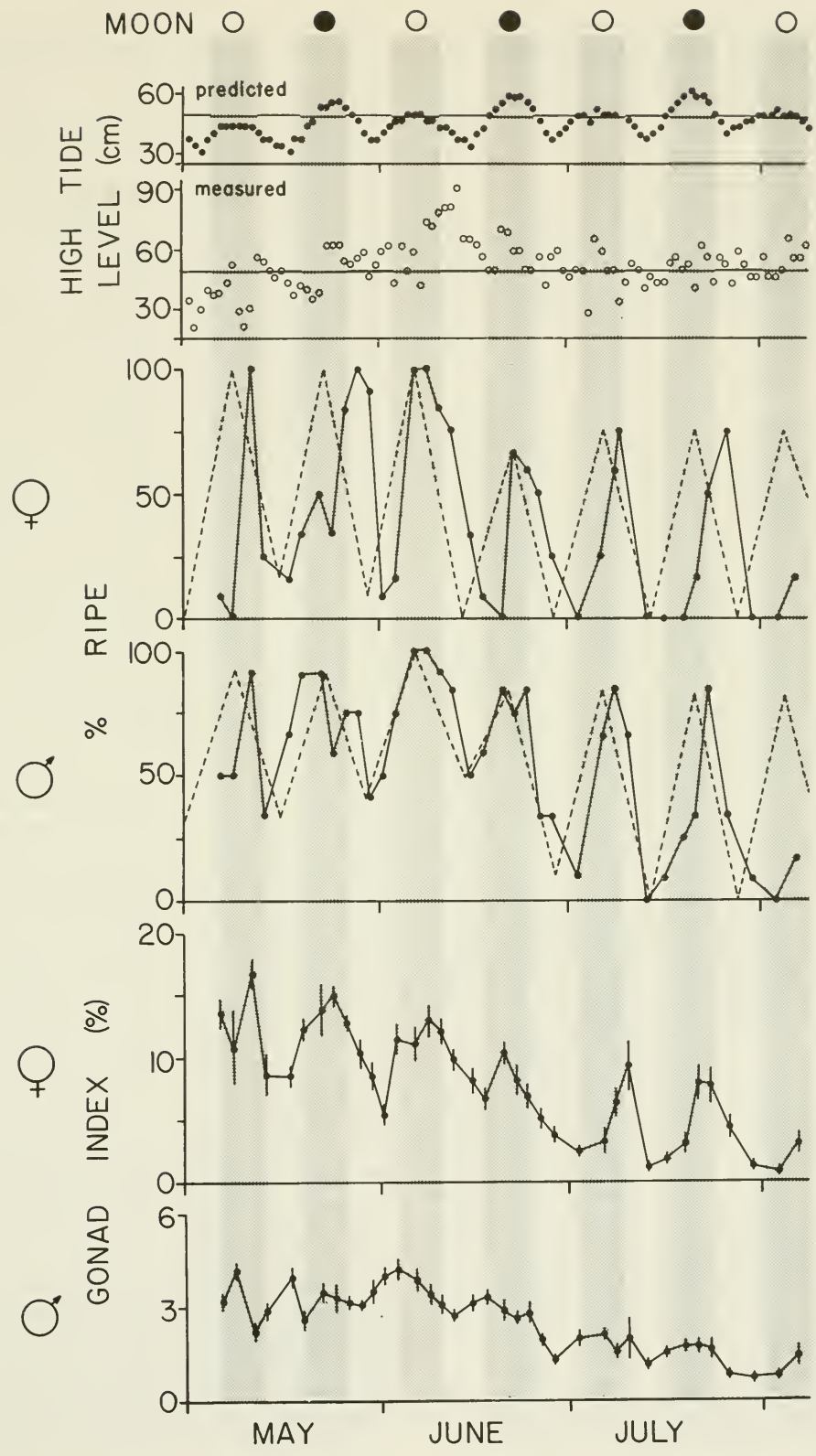
Results

Although tides in the Rhode River subestuary exhibited an approximately semidiurnal rhythm, fluctuations in measured high tide level were not correlated with predicted high tide level (product moment correlation of log transformed data for daily predicted and measured high tide, $r = 0.111$; Student's t-test for $r \neq 0$, $P > 0.2$; Fig. 1). Moreover, time series spectral analysis (Thrall and Engelman 1981) showed that measured tides exhibited only a very weak peak in spectral density at a frequency of about 12.5 d rather than the strong peak of 7.5 d exhibited by predicted tidal cycles. Cross correlation between predicted and measured tides in bivariate spectral analysis showed low and variable coherence ($P > 0.05$). Similarly, linear association of the two variables was weak, with variable phase shifts and variable coefficients necessary to fit one variable to the other. In addition, the occurrence of tides sufficiently high to flood the marsh fringing the creek (i.e., tides > 46 cm) did not occur more frequently at night than during day (χ^2 test, $P > 0.2$), nor more frequently during any particular lunar phase (χ^2 test, $P > 0.4$). High tides did not occur consistently during any 2-h period of the 24-h day at the quarters of the new or full moons (χ^2 test, $P > 0.4$). Thus, water levels in the estuary were neither predictable in amplitude within the tidal range nor related in any obvious cyclical pattern to the lunar cycle.

However, both female and male *F. heteroclitus* showed distinct semimonthly cycles in readiness to spawn from May through August (Fig. 1). Females and males also exhibited a distinct semimonthly cycle of gonad size, although the cycle of male gonad index was not as pronounced as that of females, due to the small changes in size of the testes during spawning (Fig. 1). The cycles of spawning readiness in males and females were usually in phase with the lunar cycle. Comparisons of the observed frequencies of spawning readiness with frequencies predicted by cycles with perfect semilunar periods and the same amplitudes showed no significant differences in 27 of 37 d of observation for females and 33 of 37 d of observation for males (χ^2 test, $P < 0.05$). Observed frequencies of spawning readiness over the entire study period were not significantly different from frequencies predicted by the perfect semilunar cycles for either females or males (χ^2 test, $P > 0.2$). Although six out of six peaks of spawning readiness for males occurred during the 7 d surrounding new or full moons, for females only four of the six peaks occurred during the first or last quarters of the moon, indicating that for the small numbers of peaks occurring during a reproductive season, readiness to spawn does not coincide with new and full moons (Fisher's Exact Test for number of spawning peaks occurring within the specified period, $P = 0.227$; Fig. 1). However, if the timing of the peaks in readiness to spawn is considered to lag 3.5 d after the new and full moons, then all peaks for males and females occurred within the 7 d surrounding the lagged period, indicating a significant synchronous semilunar cycle (Fisher's Exact Test on number of peaks occurring within the specified period, $P < 0.01$). Female spawning was correlated with male spawning (product moment correlation of arcsine transformed spawning frequencies, $r = 0.695$; Student's t-test for $r \neq 0$, $P < 0.001$). However, neither female nor male readiness to spawn was correlated with the measured tides (product moment correlation of arcsine transformed frequencies of spawning readiness with log transformed high tide measurements, $r = 0.184$ for females and $r = 0.272$ for males; Student's t-tests for $r \neq 0$, $P > 0.2$). Thus the semilunar cycles of spawning readiness of both sexes appeared to be synchronized, but not to be related to the tidal regime of the estuary.

The reproductive season of *F. heteroclitus* in the Rhode River-Muddy Creek estuarine system occurred from late April to September, when water temperatures were above 17°C (pers. obs.). Mean gonad indices of female and male samples declined during the season, both at the peak and at the spent phases of the semimonthly cycles (Female Gonad Index = -0.124 Day + 14.1 and Male Gonad Index = -0.035 Day + 3.83; Student's t-test for slopes $\neq 0$, $P \leq 0.05$; (Fig. 1)). The decline of mean gonad index during the season reflected two statistics. First, an increasing percentage of the population failed to initiate gonad recrudescence during successive cycles.

FIGURE 1.—Lunar phase, tidal levels, and reproductive cycles of *Fundulus heteroclitus* from May to August 1982 in a tidal creek on central Chesapeake Bay. Full moons (open circles) and new moons (solid circles) are indicated. Daily high water levels above mean low water are shown for measurements at the study site and for tidal levels predicted by National Oceanographic and Atmospheric Administration (1981). Horizontal lines indicate water level which floods the marsh adjacent to the Creek. The percentages of female and male fish which were ready to spawn are shown for each sample throughout the spawning season (solid lines), along with hypothetical spawning cycles with the same amplitudes and perfect semilunar periods in phase with the new and full moons (dashed lines). Gonad indices (mean ± SE) for females and males are also plotted for each sample.


MOON
predicted
measured
HIGH TIDE LEVEL (cm)
60
30
90
60
30
♀
100
50
0
% RIPE
♂
100
50
0
♀
20
10
0
GONAD INDEX (%)
♂
6
3
0
MAY
JUNE
JULY

None of the female fish sampled on the May spawning peaks had undeveloped gonads (individual gonad indices were all > 10%), whereas many had undeveloped gonads on the July peaks (38% of the sample for gonad weights had individual indices < 5%, and 25% of the sample tested for spawning were not ripe). Second, gonad size of fish with developed gonads declined during the season. Mean gonad indices of females with developed ovaries of the May peaks were significantly greater than those of the July peaks (15% versus 9%, respectively) (Student-Newman-Keuls test of arcsine transformed data, $P < 0.05$).

Discussion

In *Fundulus heteroclitus* and *F. confluentus*, regulation of the annual reproductive cycle is apparently dependent on changing combinations of photoperiod and temperature (Harrington 1959; Day and Taylor 1982). The decline in gonad index during the season in the present study is consistent with a similar decline observed by Kneib and Stiven (1978) and Taylor et al. (1979) and suggests that, along with physical factors, energy availability may be limiting reproductive output late in the season. Weisberg (1981) found that supplemental food increased the gonad indices of *F. heteroclitus* in Delaware salt marshes. Histological evidence shows that primary oocytes in *F. heteroclitus* can undergo complete development in one biweekly spawning cycle (Taylor and DiMichele 1980), so lag time for recrudescence of spent gonads does not account for reduced reproductive activity late in the season. *Fundulus grandis* reproduces throughout the summer in some areas of the gulf coast (Greeley and MacGregor 1983), but shows bimodal reproductive activity in spring and fall with no reproduction in midsummer in shallow ponds (Waas and Strawn 1983).

In addition to *F. heteroclitus* (Taylor et al. 1979; Taylor and DiMichele 1980), semilunar spawning cycles occur in some populations of *F. grandis* (Greeley and MacGregor 1983), *F. similis* (Greeley 1982), *F. majalis* (Tedesco et al.[4]), and probably in *F. notatus* (inferred from observations of spawning behavior in Carranza and Winn 1954). Waas and Strawn (1983) measured a weak lunar, but not a semilunar cycle in populations of *F. grandis* in two nontidal ponds and a tidal creek with lunar tides frequently overridden by wind effects. The semilunar spawning cycle in *F. grandis* has been induced in the laboratory during their reproductive season by interaction of photoperiod and tidal changes in water temperature shifting on a lunar cycle (Miller et al. 1981). Daily disturbances (netting) of *F. grandis* also apparently induces circadian gonadal responses (Weld and Meier 1982). Tidal rhythms in water turbulence and hydrostatic pressure have been postulated for lunar and semilunar reproductive rhythms in fish (Korringa 1947; Ross 1983) and for semilunar hatching in intertidal chironomid insects (Newmann 1978). Middaugh (1981) suggested that the biweekly coincidence of a high tide at the time of sunrise and/or a lunar cue may serve as a synchronizer for spawning of *Menidia menidia* in a South Carolina estuary. In contrast to *M. menidia*, which showed a precise reproductive response to diurnal tidal and lighting schedules (Middaugh and Takita 1983), *M. peninsulae* exhibited a variable and labile response in which a combination of semidiurnal interruptions of current and diel light cues was optimal at inducing spawning synchrony (Middaugh and Hemmer 1984). However, this synchrony in *Menidia* spp. had a diel period, and the laboratory experiments were not run long enough to test for lunar rhythms. Semilunar rhythms of larval hatching are well documented for several species of intertidal and estuarine crabs (see Christy 1982; Forward et al. 1982). Hatching in the mud crab, *Rhithropanopeus harrisii*, followed a semilunar and diurnal rhythm in populations from an estuary with semidiurnal and lunar tidal cycles, whereas hatching was not associated with lunar rhythms or tidal levels in an estuary with aperiodic tides (Forward et al. 1982). Moveover, Forward et al. (1982) induced circatidal rhythms in larval release in crabs from an estuary with irregular tides by transplanting them to an estuary with semidiurnal and lunar tides. However, Saigusa (1980) showed that the larval hatching cycle of a semiterrestrial crab *Sesarma haematocheir* is entrained directly by a moonlight cycle.

In the present study, in an area without a lunar periodicity in the tidal cycle, *F. heteroclitus* had a semilunar reproductive cycle which lagged the new and full moons by 3.5 d. Although the study area had tidal fluctuations with an approximately semidiurnal period, the diel timing of high tides with respect to photoperiod also did not appear to cue the semilunar reproductive cycle. Changes in currents associated with the diurnal tidal cycle may serve as a synchronizing cue for the time of day of spawning, as it does for *Menidia menidia* and *M. peninsulae*. However, while identity of the cue remains unknown, the present study indicates that tidally mediated factors such

[4]Tedesco, M., A. H. Hines, and L. A. Wiechert. 1983. Semilunar gonadal cycles in *Fundulus majalis* (Pisces: Cyprinodontidae). Technical Report of Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037.

as turbulence, hydrostatic pressure, temperature, and salinity are not responsible for synchronizing the semilunar rhythm.

Hypotheses concerning the ecological consequences and adaptive significance of semilunar cycles of larval release in *Uca* spp. and other estuarine crabs have been discussed recently by Christy (1982). His analysis indicates that convergence among estuarine crab species in the semilunar timing of larval release results in rapid seaward transport of larvae, which minimizes the effects of lethal combinations of high temperature and low salinities or intense predation in the upper estuary. However, *Rhithropanopeus harrisii* completes its larval development within the upper reaches of estuaries and shows a variable cycle of hatching, depending on tidal predictability, which may be advantageous for retention of larvae within the estuary (Forward et al. 1982). Lunar spawning cycles of insular coral reef fish may have evolved to solve similar problems of larval dispersal away from predators while assuring return of the recruits to the adult habitat (Johannes 1978; Ross 1983). Semilunar spawning cycles of *Fundulus heteroclitus*, *Menidia menidia*, *Leuresthes tenuis*, and other fish which spawn in the upper intertidal zone (Taylor and DiMichele 1983; Middaugh 1981; Clark 1925) may have the adaptive advantage of removing spawning adults and eggs from subtidal predators. Although the eggs of *F. heteroclitus* are tolerant of desiccation (Able and Castagna 1975; Taylor et al. 1977), the major advantage of the spawning site appears to be higher oxygen levels and reduced sedimentation than in the creek (Taylor and DiMichele 1983). However, spawned eggs of *F. heteroclitus* and *M. menidia* are usually found in areas inundated daily by high tides (Middaugh 1981). In the present study, 62% of the days had tides which flooded the marsh (Fig. 1), where eggs are probably deposited in the bases of leaves of *Typha angustifolia* plants (see Taylor and DiMichele 1983). Although there may be additional advantages in areas with predictable tidal fluctuations with lunar periodicity, the major advantage of semilunar spawning rhythms in *F. heteroclitus* appears to be improved fertilization success afforded by synchronized spawning.

Acknowledgments

We are grateful for the assistance of L. Wiechert, S. Hodgkins, C. Trowbridge, and K. Comtois. R. Cory and P. Dresler of the U.S. Geological Survey provided the data for measured tidal levels. R. Ross and M. Taylor provided helpful discussion. D. Correll, T. Jordan, and two anonymous reviewers provided suggestions for improvements in earlier drafts of the manuscript. This work was supported in part by the Smithsonian Work/Learn Internship Program, Maryland Department of Natural Resources, and the Smithsonian Environmental Sciences Program.

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Anson H. Hines
Kenric E. Osgood
Joseph J. Miklas

Smithsonian Environmental Research Center
P.O. Box 28
Edgewater, MD 21037

UNDERSEA TOPOGRAPHY AND THE COMPARATIVE DISTRIBUTIONS OF TWO PELAGIC CETACEANS

Prey species are not uniformly distributed. Foraging efficiency, therefore, should be maximized when effort is concentrated in areas where prey are concentrated. Cetacean food is probably most concentrated in regions of high general productivity. Because the undersea topography may be a major influence on productivity, cetacean foraging patterns may be associated with the topographic patterns of the ocean floor (Hui 1979). I report here the occurrences of two species of pelagic odontocete cetaceans, the Pacific pilot whale, *Globicephala macrorhynchus*, and the common dolphin, *Delphinus delphis*, relative to seafloor topography and to diet. Although it is not clear if the genus *Delphinus* in this region is composed of two species or one species with two subspecies, the vast majority are *Delphinus delphis* (Banks and Brownell 1969; Evans 1975). If data from more than one species are included in this study, it is assumed that any interspecies difference in distribution relative to substrate was not significant to the analyses.

Methods and Results

This study was conducted in the Southern California Continental Borderland (Fig. 1) which consists of ridges, deep troughs, and basins (Chase 1968). There were 61 survey flights totaling 22,353 km. The flights were conducted at various times, all of them during midday (1000-1500) from 1968 through 1976. Totals of 1,057 pilot whales in 38 aggregations (in January, March, April, July, October, and December) and 47,105 common dolphins in 142 aggregations (in all months of the year) were observed. The survey methods have been previously described (Hui 1979).

The data for each species were not divided into temporal subsets as in Hui (1979), but were treated as whole sets. The distribution of each species was examined relative to depth and relative to change in depth. The method of analysis has been presented in detail elsewhere (Hui 1979).

Both pilot whales and common dolphins were distributed uniformly ($P > 0.10$) throughout the depth classes but not uniformly among the Contour Index (CI) classes ($P < 0.005$). For each species there were more observations than expected over the steepest bottom topography and fewer than expected over the flattest (Table 1).

I also compared the distribution of pilot whales

among CI classes to the distribution of common dolphins. Due to the small number of pilot whale aggregations, the CI range was divided into four unequal classes to meet the statistical assumptions for chi-square analysis (Dixon and Massey 1969). The proportion of pilot whales in each of these classes

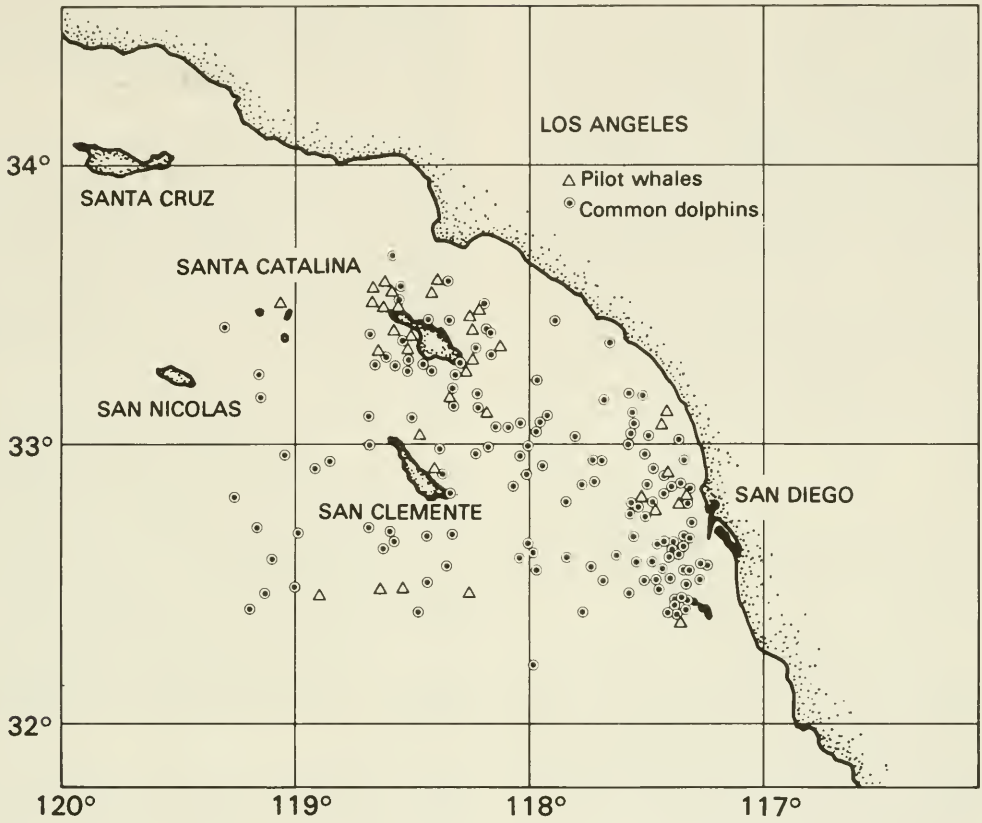

FIGURE 1.—Sightings of pilot whales, *Globicephala macrorhynchus*, and common dolphins, *Delphinus delphis*. The study area is bounded on the west by long. 120°00'W and on the east by the coast of California between lat. 34°05'N and 32°24'N. Sightings may not accurately depict the geographic distribution of these species because the survey flights were not uniformly distributed spatially or temporally. Encounters occurring outside the study area are not shown.

TABLE 1.—Distribution among contour index classes of observed and expected aggregations (see text).

Species	Contour index class	Number of aggregations		$(F-f)^2/F$
		Expected (F)	Observed (f)	
Pilot whales	0.01-19.99	13.3	1	11.38
	20.00-39.99	6.3	5	0.27
	40.00-59.99	5.2	4	0.28
	60.00-79.99	7.4	10	0.91
	80.00-99.99	5.8	18	25.66
				χ^2 = 38.50
Common dolphins	0.01-19.99	48.0	18	18.75
	20.00-39.99	23.2	27	0.62
	40.00-59.99	19.3	22	0.27
	60.00-79.99	27.2	21	1.41
	80.00-99.99	22.2	54	45.55
				χ^2 = 66.60
				χ^2 (df = 4, P = 0.005) = 14.86

was used to compute the expected number of common dolphins in that class.

The distribution of pilot whales was not the same as that of common dolphins among the CI classes ($P < 0.005$), particularly in the class for the lowest relief. Of the total chi-square value, 63% is due to proportionally more observations of dolphins than pilot whales in this one class (Table 2).

The distributions of the two sets of survey flights used to collect data for the two species were compared, but the CI range in this case was divided into 10 equal classes. The two sets of survey flights were equally distributed among the CI classes ($P > 0.10$).

TABLE 2.—Comparative distribution among contour index classes of pilot whales and common dolphins.

Contour index class	Dolphin aggregations		$(F\text{-}f)^2$
	Expected (F)[1]	Observed (f)	F
0.01-39.99	22.4	45	22.80
40.00-59.99	14.9	22	3.38
60.00-79.99	37.4	21	7.19
80.00-99.99	67.3	54	2.63
			$\chi^2 = 36.00$
			χ^2 (df = 3, $P = 0.005$) = 12.84

[1]Computed from pilot whale sightings; see text.

Discussion

In the California Bight, pilot whales and common dolphins are distributed similarly above undersea topography of high relief, but common dolphins occur more frequently than pilot whales over areas of low relief. This difference may be linked to differences in feeding habits.

Pilot whales and common dolphins have significant morphological and physiological differences that are associated with their foods and feeding methods. Pilot whales are larger (7 m vs. 2 m in length) and have fewer but larger teeth (40 vs. 200) than common dolphins (Orr 1972). Pilot whales are capable of diving to 610 m (Bowers and Henderson 1972) while common dolphins dive to 257 m (Evans 1971).

The diet of the common dolphin in the Southern California Bight includes 19 species of fish, 2 species of squid, and miscellaneous crustaceans (Fitch and Brownell 1968; Evans 1975).

In contrast to common dolphins, pilot whales appear to be stenophagous, eating primarily squid. Atlantic pilot whales, *Globicephala melaena*, eat primarily squid (*Illex illecebrosus*). The only fish reported eaten (cod, *Gadus morhua*) composes <10% of the diet (Sergeant 1962). There has been no study on the Pacific pilot whale comparable with that of Sergeant's (1962) on the Atlantic form; however, the stomachs of four wild Pacific pilot whales have been examined. They contained squid but no fish (W. A. Walker,[1] C. W. Woodhouse,[2] D. J. Seagars[3]). In captivity an Atlantic pilot whale rejected mullet (Mugilidae) and blue runner (Carangidae) fish and accepted only squid (probably *Loligo pealei*) until it was tricked into eating some herring (Clupeidae); and then the indications were that "He did not seem to digest the fish as well" (Kritzler 1949).

Squid distribution cannot be related to any particular bottom topography along the California coast because squids are not easily collected with sampling methods used in distribution studies (Mais 1974). However, it may be inferred that the narrow range of seafloor topographies visited by pilot whales reflects the narrow range of their diet and the areas where squid can be most easily caught by pilot whales.

Also concentrated over areas of canyons and escarpments are anchovies (Mais 1974), a major component of the dolphin diet (Fitch and Brownell 1968; Evans 1975). Common dolphins frequent these areas most. However, common dolphins are euryphagous. Some prey probably occur over seafloor of low relief, although this could not be confirmed from fish reports because bottom topography is not a parameter which is recorded in fish distribution studies. If some prey do occur over areas of low relief, their distribution would partially explain why dolphins occur over seafloor of low relief more frequently than do pilot whales.

My analyses show that the daytime distribution patterns of these two pelagic cetacean species are not random but are related to bottom topography. Although the distributions are similar, they are not the same. Differences in distributions may be due to the different foraging patterns but no firm conclusion can be drawn until more information is available.

Acknowledgments

I thank G. A. Bartholomew, M. F. Platter-Rieger, F. G. Wood, and two anonymous reviewers for their helpful comments; also D. J. Seagars, W. A Walker, and C. W. Woodhouse for information on the

[1]W. A. Walker, Research Associate, Section of Mammalogy, Natural History Museum of Los Angeles County, Los Angeles, CA 90007, pers. commun. July 1980.

[2]C. W. Woodhouse, Curator of Vertebrate Department, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105, pers. commun. July 1980.

[3]D. J. Seagars, Wildlife Biologist, National Marine Fisheries Service, Southwest Region, 300 S. Ferry St., Terminal Island, CA 90731, pers. commun. January 1981.

stomach contents of Pacific pilot whales. My special thanks to W. E. Evans of Hubbs Sea World Research Institute for his support and encouragement throughout this study, which was supported by ONR contract T0044 subproject RR0310201 (W. E. Evans, principal investigator), and NMFS agreement 01-6-200 11439.

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CLIFFORD A. HUI

Chemistry and Biochemistry Branch, Code 521
Naval Ocean Systems Center
San Diego, CA 92152-5000

LARVAL AND JUVENILE GROWTH OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, AS DETERMINED FROM OTOLITH INCREMENTS

The black cod or sablefish, *Anoplopoma fimbria*, has been the subject of an intensifying fishery off the west coast of North America over the last decade. Biological information on this species, however, including data on spawning, early life history, age and growth, and population structure, is relatively meager. Sablefish are widely distributed in the northern Pacific, with adults most abundant at depths of 366-915 m (Hart 1973). Mason et al. (1983) suggested that eggs are spawned and developed in waters deeper than 300 m and colder than 6°C off Canada. Juveniles occur in shallow water, however, and larvae are almost exclusively neustonic (Kendall and Clark[1]). Thus larval development and growth occur in much warmer water than that inhabited by later stages, particularly in the southern portion of the species range.

Sablefish growth has been described by Heyamoto (1962) and Pruter (1954), among others, who used scale annuli to define the growth pattern. More recent work, however, has shown that the age estimates, particularly for older, mature fish, are in error; growth is apparently much slower and longevity much greater than previously thought (Beamish and Chilton 1982). The warmer neustonic habitat of the larvae may result in different growth patterns in early life; ontogenetic changes in growth and habitat are relatively common among deeper living fishes (Boehlert 1982; Luczkovich and Olla 1983). The only observations on growth of young sablefish are those of Heyamoto (1962), who suggested that juveniles of 12-16 cm fork length (FL) were about 6 mo old. In the present study we report on the growth of field-collected larval and juvenile sablefish where age was estimated by enumerating growth increments on the otoliths.

Materials and Methods

Larval and juvenile sablefish were collected in 1981-83. Larvae were taken in 0.5 m neuston nets (Sameoto and Jaroszynski 1969) with 0.505 mm mesh, off the coasts of Oregon and Washington during May 1982 by the RV *Poseydon*. Samples were immediately preserved in 80% ethanol. After sorting,

[1]Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and northern California, April-May 1980. Processed Rep. 82-11, 44 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98102.

larvae were stored in individual vials labeled with sample number and date. Additional larvae were collected with neuston nets in May 1983 by the RV *Ekvator*. Larger juveniles (> 70 mm standard length (SL)) were taken in a small mesh purse seine deployed from 24 to 40 km off of the Oregon-Washington coasts during the summer months of 1981 (Fig. 1). Specimens were frozen on board and held until measurements and otoliths were taken. Fork lengths to the nearest millimeter were recorded for these larger juveniles and standard lengths to the nearest 0.1 mm were measured for all larvae and small juveniles. No corrections were made for potential shrinkage from preservation of young larvae, but alcohol preservation causes no noticeable shrinkage in length of anchovy larvae (Theilacker 1980). For subsequent analysis, fork lengths were converted to standard length by the relationship SL (mm) = 0.91 FL (mm) − 1.15 (n = 54, r^2 = 0.999), which was based upon specimens 21.7 to 297 mm FL.

Otoliths of larval sablefish were removed and cleaned under a dissecting microscope fitted with polarizing filters. Increments on otoliths from larvae < 26 mm SL were clearly visible from the focus to the margin (Fig. 2); these otoliths were left intact, affixed to microscope slides with histological mounting medium and cover slips, and increments were read in the sagittal plane (see Taubert and Coble 1977 for terminology). For larger larvae and most juveniles, a sagittal section of the otolith provided the clearest increments. The left otolith of every pair was mounted in histological medium on a microscope slide and the

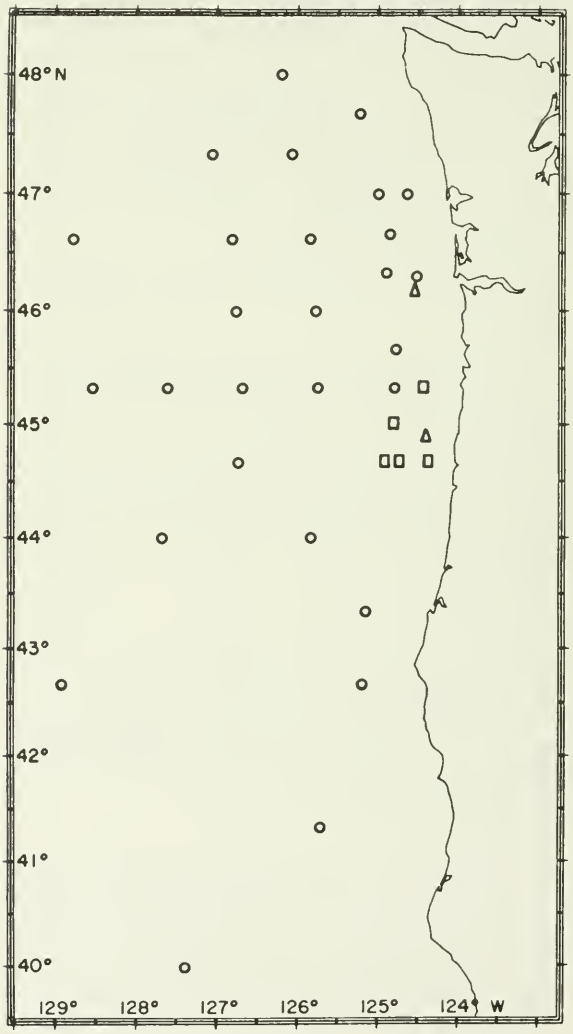

FIGURE 1. – Distribution of *Anoplopoma fimbria* samples, along the Pacific coast, used for age and growth analysis. Circles represent the neuston samples taken during May 1982, triangles represent the purse seine samples taken during summer 1981, and squares represent the 1983 neuston samples.

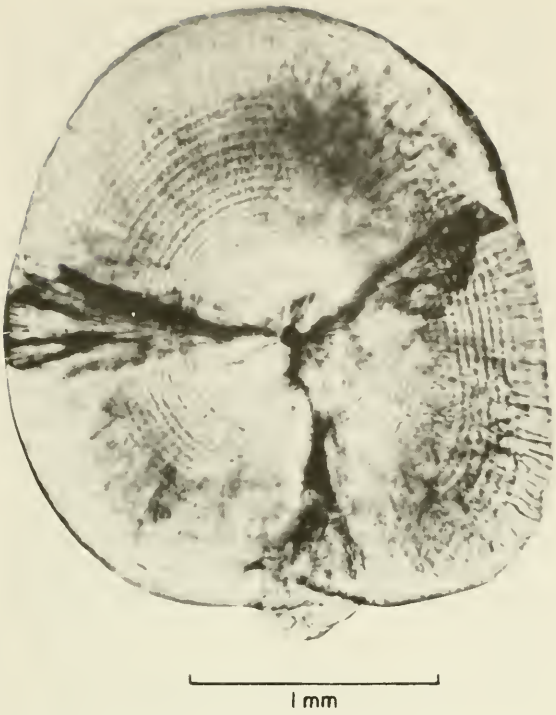

FIGURE 2.—Sagitta otolith from a larval *Anoplopoma fimbria* (22.0 mm SL; duplicate increment counts were 37 and 40 d). Scale bar = 0.1 mm.

internal surface was ground until the focus was visible. The microscope slide was heated and the section was turned over to expose the external surface. Grinding and polishing continued, while care was taken to insure that material was not lost from the margin. The result was a clear, thin section of the otolith in the sagittal plane. For some of the larger juveniles (> 100 mm SL), transverse sections were cut from the otoliths using a diamond saw, mounted on microscope slides, and ground to make the increments clear. All otoliths were read under a compound microscope at 400× or 1,000× magnification. Two independent counts were made for each otolith. These counts were made at least 2 wk apart; the age assigned to each specimen was the mean of the two counts.

Increments, comprised of adjacent light and dark ring pairs, were distinct and clear in the smallest otoliths (Fig. 2), but interpretation became more difficult as the increments became progressively smaller and as changes in growth patterns occurred in the otolith structure of the older specimens. There was no evidence of subdaily patterns in the increments, and each increment was assumed to represent 1 d. Support for the daily deposition of increments was provided by data on three live juvenile sablefish held in the laboratory (Table 1). The specimens were captured by neuston net off Newport, OR, and transported to the laboratory where they were fed to satiation daily on *Artemia*. A check, apparently associated with capture and transfer to the laboratory, was evident on the otolith of each fish. The numbers of increments past this check corresponded closely to days captive; the minor differences are attributed to counting error and/or difficulty in interpretation of the check (Table 1). We thus consider the increments to be deposited with a daily periodicity. Hereafter increment counts will be equated with days after first increment formation; as we discuss later, first increment formation may occur at first feeding.

Data from the 1982-83 larval collections and the 1981 juvenile collections were fitted separately with simple linear regressions. Nonlinear curves (exponential, logistic, and Laird-Gompertz) were fitted to combined data with the NLIN procedure on the SAS[2] statistical package (SAS Institute, Inc. 1982).

TABLE 1.—Growth and increment formation in captive specimens of *Anoplopoma fimbria*. L_1, L_2; standard length (mm) at capture and death, respectively.

Capture date	L_1	L_2	Days captive	Increment past check	Total increments
2 May 1983	19.9	60.4	31	31	63
17 May 1983	14.1	53.4	40	38	95
24 May 1983	53.8	109.7	32	33	87

Results and Discussion

This study considers a total of 105 individuals, including 71 larvae and juveniles (9.8 to 41.2 mm SL) from the 1982 neuston collections, 21 juveniles (102.8 to 259.6 mm SL) from the 1981 purse seine collections, and 13 larvae (10.4 to 25.3 mm SL) taken in the 1983 neuston collections. Mean increment counts ranged from 9 increments for the youngest larva to 180 increments for the oldest juvenile. The abundance of larval sablefish in the neuston (Kendall and Clark footnote 1) at such young ages suggests that larvae move rapidly after hatching from the deep spawning region rather than early growth occurring at depths as suggested by Mason et al. (1983). The difference between the two increment counts for each otolith increased with increasing count, but the coefficient of variation remained the

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

same for the two ranges. For the larvae collected in 1982, with an overall mean of 30.8 increments, the mean difference was 1.67 increments (n = 71, standard deviation (SD) = 1.45). For the 1981 juvenile collections, with overall mean of 109.5 increments, the mean difference between the two estimates was 6.57 increments (n = 21, SD = 5.03).

Growth rates of field-collected larval and juvenile sablefish differ considerably. The data for the 1982 larval collections is described by the line

$$\text{SL} = 0.375\ (\text{age, d}) + 5.27$$
$$n = 71,\ r^2 = 0.838,$$

suggesting a mean growth rate for small larvae of 0.375 mm/d and an intercept of 5.27 mm, which coincides with the size of newly hatched larvae (Mason et al. 1983). Similarly the 1981 juvenile data is described by the line

$$\text{SL} = 1.469\ (\text{age, d}) - 0.926$$
$$n = 21,\ r^2 = 0.822,$$

suggesting a mean growth rate of 1.47 mm/d. Certain of these growth differences may have been a function of gear selection. If net avoidance is a function of fish size, as for most other planktonic organisms (Barkley 1972), then the oldest specimens taken in the neuston gear may have been only the slow-growing members of that cohort. Alternatively, interruptions of increment formation, resulting in underestimates of age, may occur. This has been observed for some species by Geffen (1982). In the laboratory specimens, however, one individual (L_2 = 60.4 mm SL, Table 1) ceased eating for 5-6 d, became emaciated, and died. The last five increments near the margin were smaller than the remainder, but the 1:1 correspondence of days to increments suggests that increment formation continued.

Estimated age-at-length data from all years were combined to describe the growth of sablefish to an age of about 200 d. Comparing exponential, logistic, and Laird-Gompertz growth models, the best fit (as judged by residual sums of squares) was provided by the Laird-Gompertz growth model (Fig. 3) in the form:

$$L_t = L_0\ (A_0/\alpha)\ (1 - \exp(-\alpha t))$$

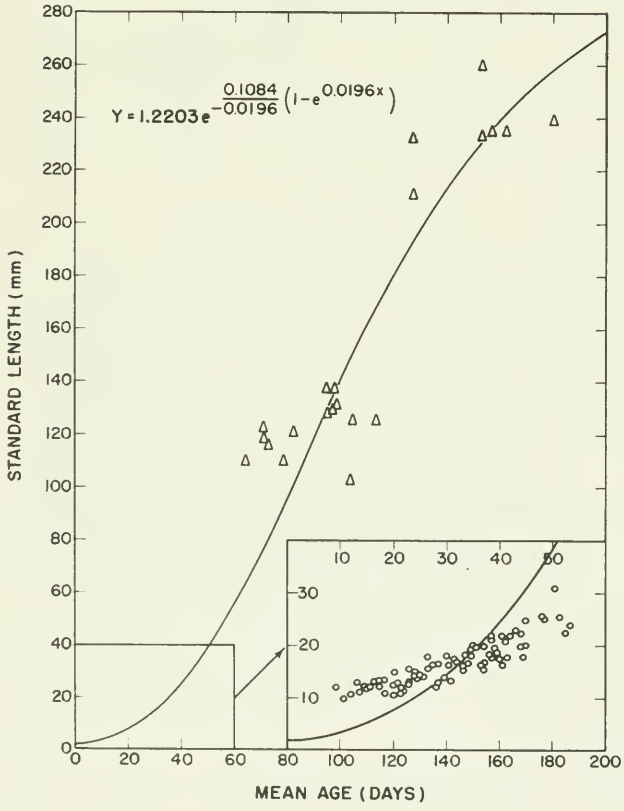

FIGURE 3.—Estimated age at length for all *Anoplopoma fimbria* in the study. Specimens taken in neuston nets (n = 84, including the 13 from 1983) are represented by circles, 1981 juvenile specimens from purse seine collections (n = 21) are represented by triangles. The equation and line represent the least squares fit of the Laird-Gompertz growth model.

where L_t = standard length (mm) at age t (d), L_0 = initial length (y-intercept), and A_0 and α are fitted parameters (Table 2).

This sigmoid curve suggests relatively slow growth to an age of about 50 d and a length of about 25 mm SL, followed by rapidly accelerating growth through the juvenile stage, an inflection point at 113.2 mm, and an asymptotic length near 307.8 mm. Since sablefish achieve lengths to 100 cm (Hart 1973), these results should not be extrapolated beyond the ages in the present study. Also, the predicted fit of zero age individuals (L_0) is 1.22 mm SL (Table 2; Fig. 3). This value does not accurately reflect the length of sablefish at hatching. Egg size in sablefish ranges from 1.8 to 2.2 mm and newly hatched larvae are 5 to 6 mm (Mason et al. 1983). If daily increments are first laid down at first feeding as in some other species (Laroche et al. 1982), then this intercept is clearly an underestimate. Mean egg size suggests a length at first feeding of about 8 mm (Shirota 1970). The smallest larva taken in the present study was 9.8 mm SL (Fig. 3). This part of the curve may be related to the inclusion of the older, slower growing neustonic specimens. Another factor may be effects of shrinkage; small specimens were preserved in ethanol, older juveniles frozen. The magnitude of shrinkage for *A. fimbria* is unknown, but capture and preservation of other fish larvae causes shrinkage which decreases with increasing age or size (Theilacker 1980). Thus increases in actual length for small individuals may have been relatively greater, changing the fitted equation and possibly increasing the length at time zero (Fig. 3).

Heyamoto (1962) estimated growth for young sablefish, suggesting that specimens 12.3 to 16.4 cm FL (11.1 to 14.8 cm SL) were 6 mo old. His data, however, were based upon estimating the age at collection by difference between capture and an assumed spawning season. In our study, 6-mo-old specimens were > 24 cm SL. The specimens captured by Heyamoto (1962) were taken by trawl in 320 to 412 m, much deeper than the epipelagic juveniles in our study. Beamish et al. (1983) used daily increments as part of a study to validate annulus formation in sablefish. In nine specimens 23 to 27 cm FL (208 to 245 mm SL), they observed from 270 to 350 (mean 313) increments but suggested that the fish were 1 yr old due to the inability to count all increments. Based upon our growth curve (Fig. 3), their ages would be overestimates.

Recent observations of laboratory growth are in substantial agreement with growth described by our curve. Shenker and Olla[3] found average growth rates as high as 2.3 mm/d for juvenile sablefish fed ad libitum. These fish were near the lengths where our curve predicts fastest growth (2 mm/d, Fig. 3). High growth rates were also observed for fish smaller than 25 mm, where our data suggest relatively slow growth. Grover and Olla[4] noted starvation of field-collected sablefish larvae based upon morphological criteria; thus food probably limits sablefish growth in the field. This species apparently has a great scope for growth given high laboratory rations or patches of high prey density in the field.

TABLE 2.—Fitted parameters of the Laird-Gompertz growth model for larval and juvenile *Anoplopoma fimbria* in the present study. The curve is fitted to all larvae and juveniles (N = 105) based upon counts of otolith increments.

Parameter	Estimate	Asymptotic standard error
L_0	1.2203	0.4675
A_0	0.1084	0.0146
α	0.0196	0.0015

The distribution of dates of first increment formation were estimated by back calculating from the ages of all specimens in our study. Since larvae and juveniles were from different years and sampling gears, it is possible that differences would be observed in this distribution. Since the plankton gear selects for smaller larvae due to avoidance by later stages, the results could be biased if the entire spawning season were not sampled. The median dates for the 1982 larvae (8 April) and the 1981 juveniles (18 March), however, were similar. Thus all 105 samples were combined and the distribution of the dates of first increment formation plotted (Fig. 4). The distribution has a mode in early April. If the first increment is formed in association with first feeding, as in most other species studied (Brothers et al. 1976; Taubert and Coble 1977; Laroche et al. 1982), then the spawning dates would precede the distribution in Figure 4. Ware (1975) provided an egg size-incubation time relationship for fishes; sablefish, with a 2 mm egg, would have an incubation time of 13 d. If a similar time is spent in yolk absorption before first feeding, peak spawning would occur in early March. This generally agrees with most other reports of the spawning season for *A. fimbria*.

[3]Shenker, J., and B. L. Olla. Laboratory growth and feeding of juvenile sablefish, *Anoplopoma fimbris*. Unpubl. manuscr.

[4]Grover, J., and B. L. Olla. Field evidence for starvation of larval sablefish, *Anoplopoma fimbria*. Manuscr. in prep. Northwest and Alaska Fisheries Center, Newport Field Office, National Marine Fisheries Service, NOAA, c/o Marine Science Center, Marine Science Drive, Newport, OR 97365 (direct correspondence to B. L. Olla).

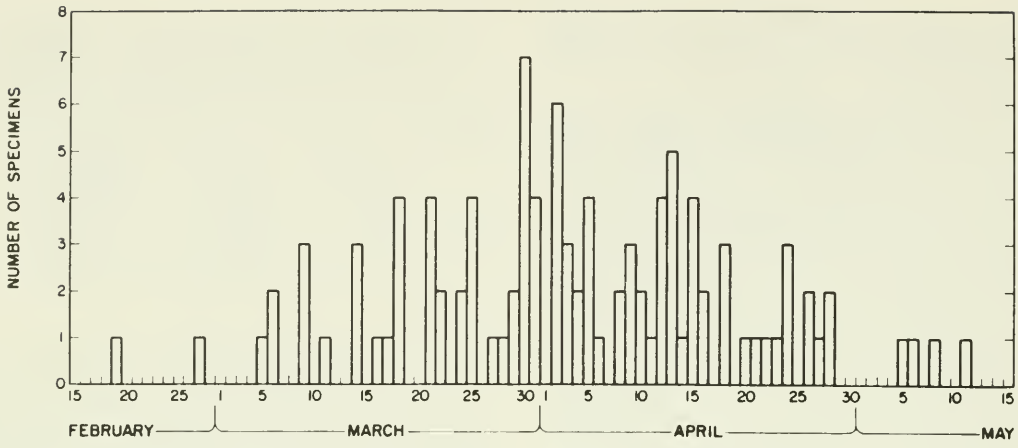

FIGURE 4.—Distribution of dates of first increment formation for *Anoplopoma fimbria*, determined by back-calculations using age and collection date.

Phillips (1958) defined the peak spawning season off California to be January-February. Bell and Gharrett (1945) suggested that the spawning season was around December off Washington based upon fishermen's observations and the presence of spent females in January. Farther north, Thompson (1941) observed ripe females and fertilized eggs in March at Cape St. James (lat. 51°45'N). More recent work has shown that the spawning season off British Columbia occurs in January to February with the peak of spawning in February (Mason et al. 1983).

Our observed growth rates for *A. fimbria* during the first 6 months of life are high for a temperate-subarctic species, yet are clearly below the potential growth rate as shown in the laboratory (Shenker and Olla footnote 3). Similar but lower laboratory growth rates (1.2 mm/d) were observed for 100 to 150 mm juvenile red hake, *Urophycis chuss*, by Luczkovich and Olla (1983). Both of these species contrast markedly with larval juvenile growth in other taxa. Boehlert and Yoklavich (1983), for example, summarized laboratory and field growth measurements for 13 species in the genus *Sebastes* and noted growth rates ranging from 0.092 to 0.590 mm/d. Young sablefish thus utilize the neustonic and pelagic environment to rapidly reach sizes at which migration to the benthic adult habitat occurs.

Acknowledgments

This work was supported by the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Seattle, WA, through contracts 81-ABC-00192-PR6 and 83-ABC-00045. We thank A. W. Kendall, Jr., W. G. Pearcy, and J. Shenker for providing specimens for this study, Chris Wilson for technical assistance with otolith preparation, and R. Methot for reviewing the manuscript.

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George W. Boehlert

College of Oceanography and Marine Science Center
Oregon State University
Newport, OR 97365
Present address:
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 3830
Honolulu, HI 96812

Mary M. Yoklavich

College of Oceanography and Marine Science Center
Oregon State University
Newport, OR 97365

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REGIONAL VARIATIONS IN THE GROWTH AND AGE COMPOSITION OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

R. H. Parrish,[1] D. L. Mallicoate,[1] and K. F. Mais[2]

ABSTRACT

Data from the Sea Survey Program conducted by the California Department of Fish and Game were analyzed to describe regional variations in growth and age composition of northern anchovy, *Engraulis mordax*. Juvenile growth appeared to be greater at higher latitudes and in the offshore portion of the Southern California Bight. Adult growth was less variable; however, there were statistically significant differences between regions. In addition, the growth rate for the southern stock was markedly lower than that of the central stock. This difference in growth rates was used to characterize the area of overlap between the two stocks. Age composition varied with depth of water and geographical location within the Southern California Bight and with latitude. Young-of-the-year and yearling fish were found in larger proportions in shallow water and in the southern and inshore areas of the Southern California Bight. Age compositions of northern anchovies sampled in the California and Mexican purse seine fisheries were compared with those of the Sea Survey Program. This comparison suggests that the present California area restrictions, which exclude the fishery from the nearshore area, greatly reduces the number of young fish in the catch.

The purpose of this study is to describe regional variations in growth and age composition of the northern anchovy, *Engraulis mordax*. Data for the study were taken by the Sea Survey Program of the California Department of Fish and Game. Mais (1974) described this program and analyzed the data for the most common species taken in the survey. This report is an extension of Mais' work and focuses on geographical variations in age composition and growth rates and on depth variations in age composition.

Meristic and morphometric (McHugh 1951) and electrophoretic (Vrooman et al. 1981) studies on the stock structure of the northern anchovy suggest that there are three stocks (northern, central, and southern) and that the boundaries between the stocks occur in central California and central Baja California. There is also recent evidence (Parrish[3]) of a fourth stock which spawns in the fall in central California and in the northern and offshore areas of the Southern California Bight.

Mais (1974) showed that the southern stock of northern anchovies was smaller at age than the central stock. In addition, northern anchovies are known to be larger off central California than off southern California (Collins 1969; Mais 1974; Mallicoate and Parrish 1981), and they are larger in the offshore areas of the Southern California Bight than in the inshore areas (Mais 1974). These differences could be due to varying growth rates between regions, varying seasonality of spawning, varying age compositions, size-specific migration, or a combination of these factors.

Tagging experiments have shown that northern anchovies move from southern California to central California, from central California to southern California, and from southern California to Ensenada, Mexico; there is a northerly movement in summer and a southerly movement in winter (Haugen et al. 1969). Mais (1974) found northern anchovies to be distributed more offshore in some years and more inshore in other years, and he found them concentrated closer to shore and in the northern part of the Southern California Bight during the fall months. Mais (1974) suggested that northern anchovies begin an offshore and southeastward movement in late winter, which coincides with the onset of major spawning activity. These movements of anchovy may affect the measurement of growth rates and age compositions within the different regions.

METHODS

The data used in the study were taken from north-

[1]Southwest Fisheries Center Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942.

[2]California Department of Fish and Game, 1301 West 12th Street, Long Beach, CA 90813.

[3]Parrish, R. H. 1983 Evidence for a fall spawning anchovy stock. Paper presented at 1983 CalCOFI Conference.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

ern anchovies caught by midwater trawl. The gear and sampling procedures are described by Mais (1974). The data set covers the period 1966-1983 and consists of 101 cruises. Twenty-three cruises extended north of Point Conception, 77 cruises occurred in southern California and northern Baja California, and 8 cruises extended into southern Baja California. Several cruises extended into more than one region. There were a total of 4,166 trawl hauls, of which 3,017 contained anchovies. Standard lengths were normally taken from about 25 anchovies in each trawl haul in which they occurred; otoliths, for aging, were usually taken from a subsample of up to 10 fish. A total of 60,082 northern anchovies were measured, of which 20,772 were aged by California Department of Fish and Game personnel with methods developed by Collins and Spratt (1969).

For purposes of determining age composition and growth rates of northern anchovies, it was assumed that February was the birth month of all fish sampled. Anchovies off California and Baja California have a peak in spawning in February-March; however, some spawning does occur all year (Ahlstrom 1966). The age determinations used in this report are, of course, not accurate to the month. They are based on the number of annuli, the seasonality of annuli formation, an assumed February birth month, and the month the fish were caught. Annuli formation occurs in May in California (Collins and Spratt 1969). A 1-yr-old anchovy would therefore be an anchovy caught in February with no annuli on its otoliths. A 1½-yr-old anchovy would be a fish with one annuli which was caught in August. An anchovy born in February would be 15 mo old when its first annuli was formed. An anchovy spawned in September would be 8 mo old if it formed its first annuli in its first May and 20 mo old if it formed its first annuli in its second May.

Differences in growth between geographical regions were compared by linear regression analyses which included anchovies of 1½ yr of age and older. Evaluation of the relationship between age composition and water depth in the area of capture was made by grouping the samples into depth strata. The strata were established partially on the number of observations.

To determine growth rates, the data were processed with a computer program (Mallicoate and Parrish 1981) which calculates and plots the mean length, standard deviation of length, and length range by age and month. The program also tabulated the number of observations by age and month; these data were used for determining age composition.

Our preliminary analysis of the sea survey data showed an alongshore cline in the mean length of northern anchovies (Fig. 1). It also revealed a bias in the selection of fish to be aged. Aged fish were generally larger at all latitudes than were the unaged fish. This bias is apparently due to a consistent tendency for samplers to pick larger anchovies for the subsample which was aged. Anchovies < 100 mm SL were particularly susceptible to not being selected for aging (Table 1). On checking with the field biologists who took the data, we found a second source of bias which occurred only in trawl hauls of exclusively small fish. When trawl hauls were considered by the sampler to be "obviously" all young-of-the-year fish, there was a tendency not to take otoliths for age determination. These sampling biases affect the analyses of age composition presented in this report but do not affect the growth analyses.

TABLE 1.—Two types of length bias in sampling northern anchovies in the Sea Survey Program.

Standard length (mm)	No. fish measured	No. fish measured in hauls sampled for otoliths	No. otolith samples	[1]Bias 1	[2]Bias 2
<70	2,174	1,275	460	0.59	0.36
70-80	2,366	1,939	684	0.82	0.35
80-90	4,667	4,241	1,667	0.91	0.39
90-100	7,077	6,367	2,498	0.90	0.39
100-110	8,988	7,875	2,997	0.88	0.38
110-120	12,058	10,834	4,164	0.90	0.38
120-130	11,744	10,462	4,215	0.89	0.40
130-140	7,390	6,456	2,748	0.87	0.43
140 +	3,619	3,036	1,339	0.84	0.44
Total	60,082	52,484	20,772		

[1]Bias 1 is the decision to sample for otoliths (i.e., the proportion of fish in trawl hauls which were sampled for otoliths).

[2]Bias 2 is the selection of larger fish by the sampler (i.e., the proportion of fish in trawl hauls, which were sampled for otoliths, for which otolith samples were taken).

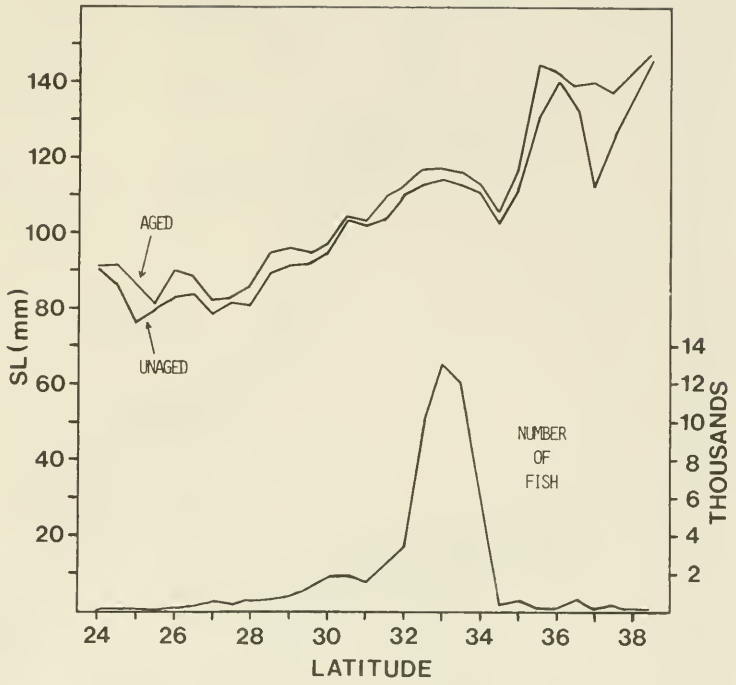

FIGURE 1.—Mean length of aged and unaged northern anchovies and the number of anchovies by half degree of latitude.

The data were inadequate to calculate growth curves or age composition on the one-half degree of latitude interval used in Figure 1; therefore, geographical regions were selected based partially on the number of observations. For example, the southern and central Baja California and central California areas, which had fewer samples, were more widely spaced than the southern California and northern Baja California areas. Nearly all of the anchovy samples taken south of lat. 32°N or north of lat. 34°N were taken within one-half degree of the coast. The lat. 32°-34°N area included a large amount of samples taken further than one-half degree from the coast. This area, the Southern California Bight, contains numerous islands and basins; we, therefore, divided it into regions which approximate the natural basins described in Emery (1954) (Fig. 2).

RESULTS

Growth

Earlier studies on northern anchovies from British Columbia (Pike 1951), northern California (Waldvogel 1977), central California (Clark and Phillips 1952), and southern California (Spratt 1975) showed considerable variation in their growth (Fig. 3A). Anchovies in British Columbia, lat. 49°N, and northern California, lat. 41°N, are of the northern stock (Vrooman et al. 1981) and have a summer spawning season. Anchovies in southern California, lat. 33°N, are of the central stock, whereas those in central California, lat. 36°N, are considered to be a mixture of northern and central stocks (Vrooman et al. 1981); anchovies in both southern and central California have a late winter (February-April) spawning season (Parrish footnote 3). Anchovies in British Columbia were the fastest growing of all the four areas in their first year of life, whereas anchovies in northern California were the slowest. Anchovies in central and southern California showed similar growth rates after their first year of life; however, the growth rate of anchovies in central California was greater than the growth rate of those in southern California in their first year.

Our study shows that the growth of anchovies has a distinct geographical pattern. Anchovies sampled in the Central California region (CC) and the offshore area of the Southern California Bight [i.e., San Nicolas (SN) and Tanner and Cortez Banks (TCB) regions] have the fastest juvenile growth (Fig. 3). Anchovies in these areas attain an average length of 120 mm before they are 1½ yr old. In the inshore areas of the Southern California Bight and in Baja California there is a continuous decline in the growth rate associated with decreasing latitude (Figs. 3, 4). Anchovies reach a mean length of 120 mm at about age 2 in the Santa Barbara Channel region (SBC)

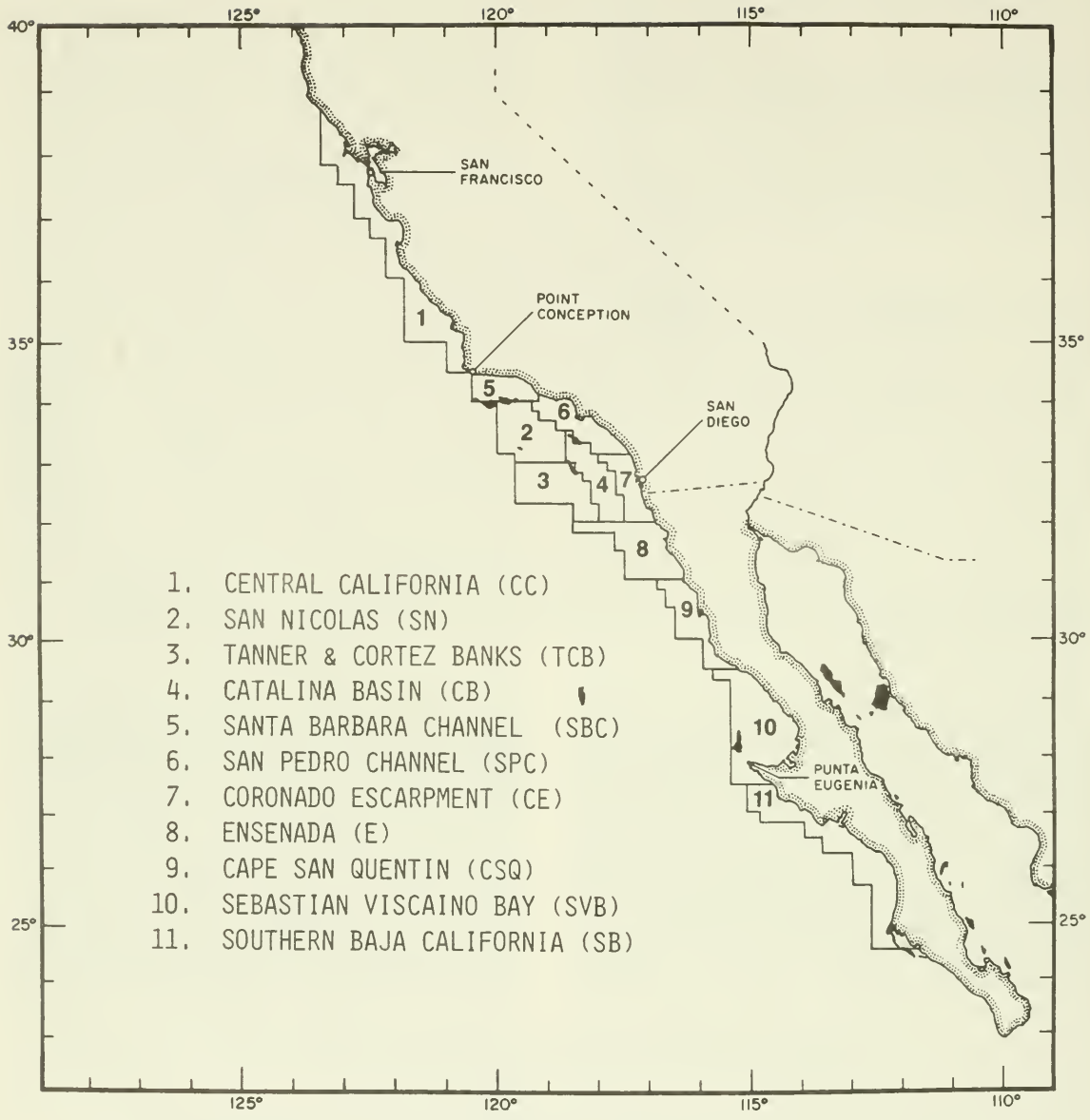

FIGURE 2.—Geographical regions for which the growth and age composition of northern anchovies were determined.

and in the remaining offshore region, Catalina Basin (CB). In the San Pedro Channel (SPC), Coronado Escarpment (CE), and Ensenada (E) regions anchovies reach 120 mm at about age 3. In the Cape San Quentin (CSQ) and Sebastian Viscaino Bay (SVB) regions anchovies reach 120 mm at about age 4 or later.

The Cape San Quentin (CSQ), Sebastian Viscaino Bay (SVB), and Southern Baja California (SB) regions include anchovies from both the central and southern stocks, and there are marked differences in their growth (Fig. 4). Anchovies from the southern stock appear to reach an asymptotic mean size of about 92 mm, whereas those from the central stock continue to grow throughout their lives. Note the occurrences of 2- to 4-yr-old fish with monthly mean lengths of about 92 mm (Fig. 4 CSQ, SVB, SB). Assuming that stocks can be identified by size at age, the Cape San Quentin region appears to be dominated by the central stock; however, the

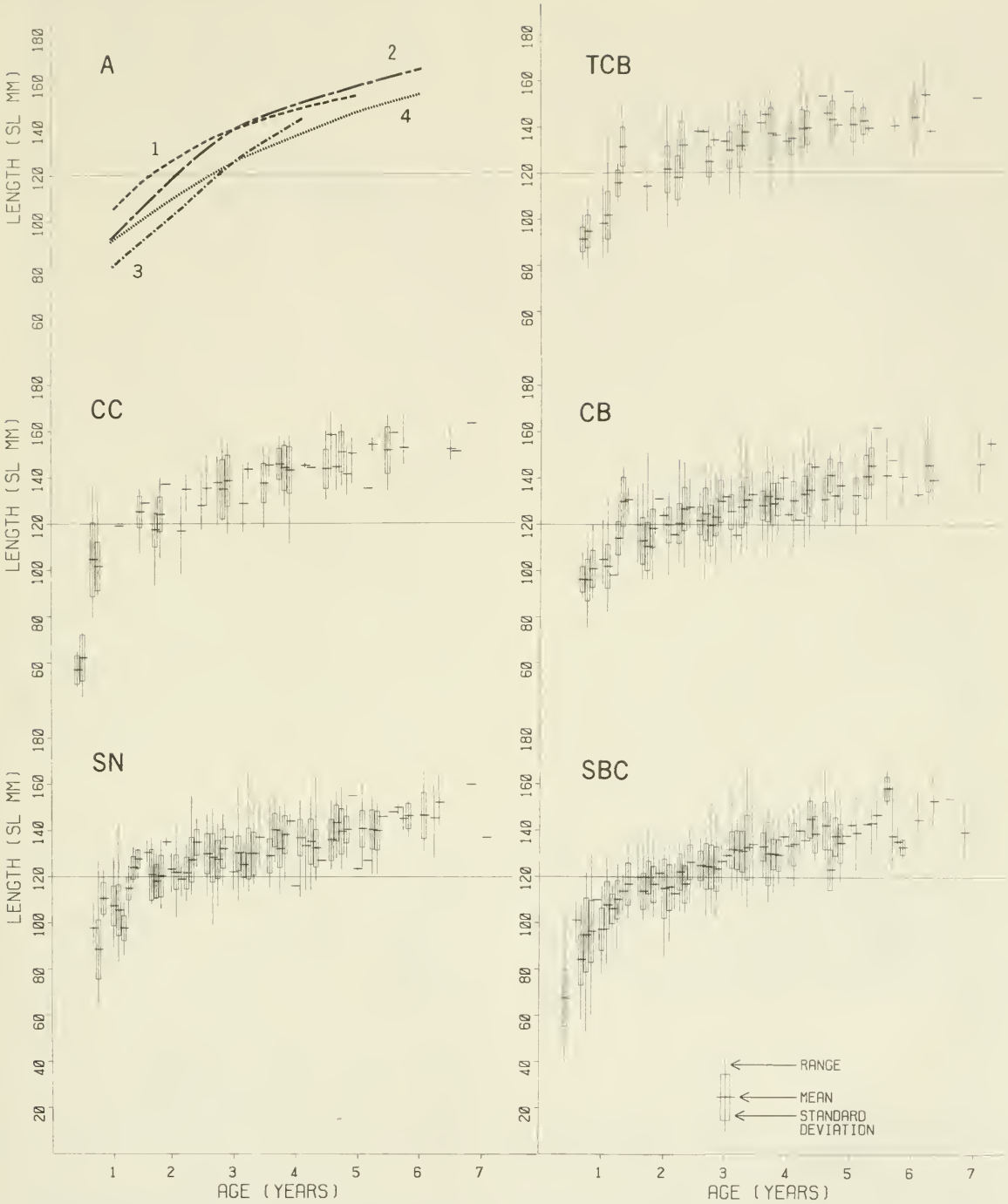

FIGURE 3.—Age-length relationships of northern anchovies taken in A. Earlier studies 1) British Columbia (Pike 1951), 2) Central California (Clark and Phillips 1952), 3) Northern California (Waldvogel 1977), and 4) Southern California (Spratt 1975), CC, Central California; SN, San Nicolas; TCB, Tanner and Cortez Banks; CB, Catalina Basin; SBC, Santa Barbara Channel.

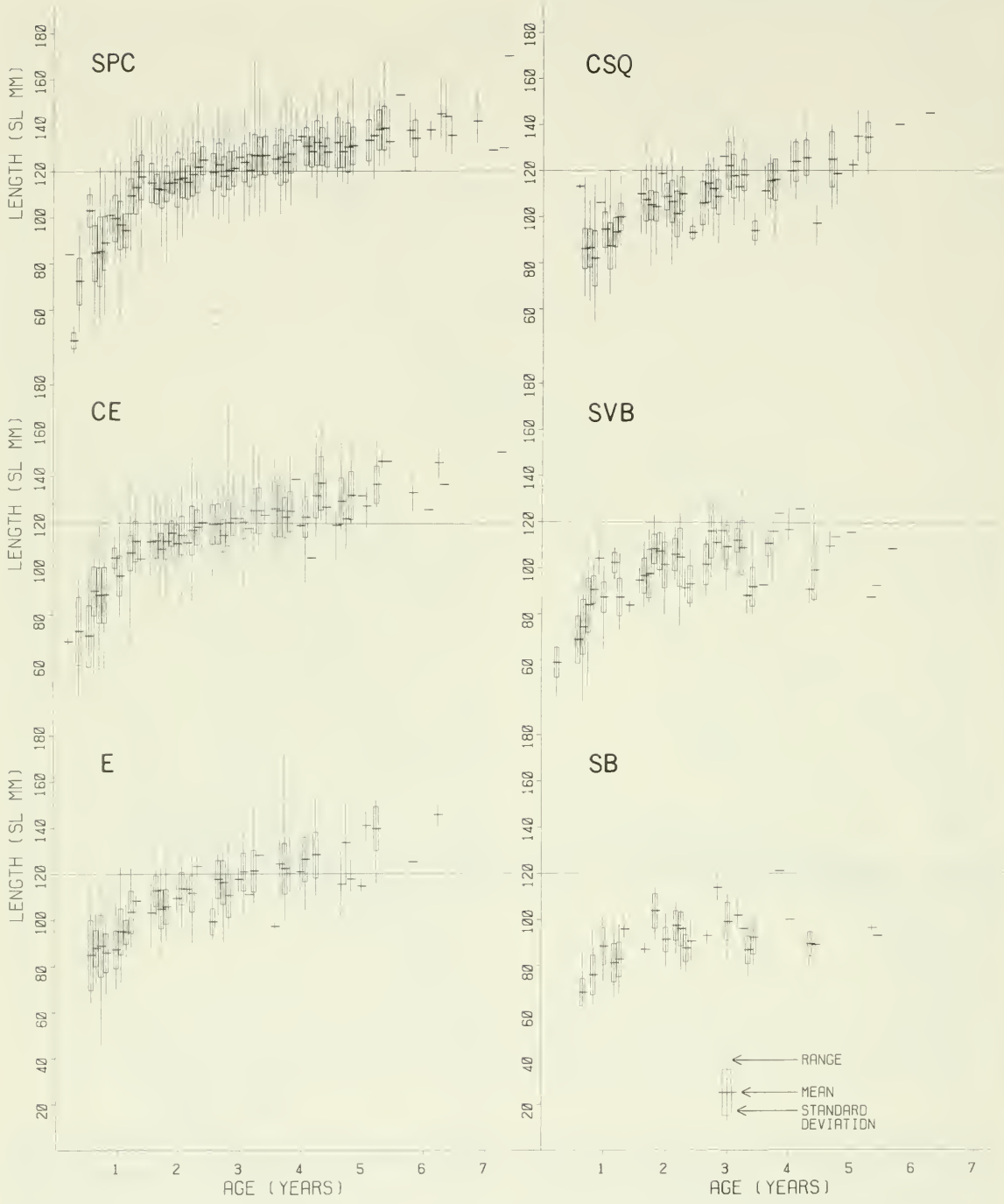

FIGURE 4.—Age-length relationships of northern anchovies taken in SPC, San Pedro Channel; CE, Coronado Escarpment; E, Ensenada; CSQ , Cape San Quentin; SVB, Sebastian Viscaino Bay; and SB, Southern Baja California.

southern stock does extend into this region. The most northerly trawl sample which could be identified, by size at age, as southern stock was a June 1971 sample taken at lat. 30.3°N. Southern and central stock anchovies broadly overlap in the Sebastian Viscaino Bay region; however, the region is occupied principally by the southern stock in the summer and by the central stock in the fall and winter. The Southern Baja California region is dominated by the southern stock; however, central stock anchovies, as identified by size at age, were taken as far south as lat. 26.5°N in November 1967. The fact that the central stock is the farthest south in winter and the southern stock the farthest north in summer suggests that the separation of the stocks is aided by different environmental preferences, possibly temperature.

The Central California region is an area of overlap between the northern and central anchovy stocks. In addition, as previously mentioned (Parrish footnote 3), a fall spawning stock may occur in central California and the offshore areas of the Southern California Bight. Vrooman et al. (1981) did not have any samples south of Monterey in central California or from the offshore and northern areas of the Southern California Bight. Samples from these areas may consist of a mixture of different stocks with different spawning seasons. Our assumption of a February birth month in these areas must therefore be evaluated.

Regression Analysis

Growth in length of anchovies in the size range sampled by the Sea Survey Program (i.e., 40-180 mm SL) can be divided into two phases. The early, juvenile phase extends until the fish are about 1 yr old. Methot (1981) found that in the Southern California Bight juvenile growth averages about 9 mm/mo, and it is at a maximum when the fish are between 40 and 50 mm SL. The second, adult phase extends from a little over 1 yr old until death. Growth during this phase is more than an order of magnitude less than the early phase (i.e., 0.48-0.69 mm/mo). Examination of the age-length relationships (Figs. 3, 4) in the central stock shows that growth in the adult phase is essentially linear. Therefore, we used linear regressions to compare growth of anchovies from different regions. These analyses included only fish of 1½ yr of age and older. This model has several advantages for comparing the growth during the two phases described above. By limiting the model to the linear segment of the age-length relationships, the slopes of the regressions can be used to compare the regional variations in growth rate during the adult phase. Another advantage is that the expected length at 1½ yr of age can be used to compare regional variation in growth during the juvenile phase.

Juvenile Growth

In the area occupied by the central stock, growth during the juvenile phase shows considerable variation among regions. There were significant differences in growth to age 1½. Fastest growth occurred in the north, and the slowest was in the south (Table 2, Fig. 5). Mean standard length at 1½ yr of age was 123.6 mm in the Central California region, 113.4 mm in the San Pedro Channel region, and 103.6 mm in the Cape San Quentin region. The three southernmost Baja California regions contain mixtures of the central and southern stocks; therefore, data from these regions were divided into central and southern stock sets, based on length and month, for the analyses. In contrast to those of the central stock, anchovies of the southern stock attain only 91.8 mm by age 1½. Within the Southern California Bight there is also an inshore-offshore gradient, with faster juvenile growth in the offshore regions and slower growth in the inshore regions (i.e, lengths at age 1½ in the Coronado Escarpment, Catalina Basin, and Tanner and Cortez Banks regions were 110.5, 116.4, and 119.2 mm respectively).

An analysis of covariance showed that the differences in size at age 1½ are not significantly different ($\alpha = 0.01$) in two pairs of regions. The San Nicolas region (120.4 mm at age 1½) and the Tanner and Cortez Banks region (119.2 mm) are the first pair, and the Catalina Basin region (116.4 mm) and the Santa Barbara Channel region (116.2 mm) are the second pair. In all other pairs of regions, size at age 1½ is significantly different at the $\alpha = 0.0001$ level.

Adult Growth

The regressions demonstrate that growth during the adult phase is relatively constant between the different regions occupied by the central stock, with slopes varying from a low of about 6 mm/yr to a high of about 8 mm/yr (Table 2). In contrast, anchovies of the southern stock have essentially no adult growth after age 1½ (i.e., slope = 0.07 mm/yr).

Although the differences in adult growth between regions is not large, there are statistically significant differences (Table 3). The San Nicolas region and the Tanner and Cortez Banks region have adult growth

TABLE 2.—Regression parameters and statistics for the relationship between age and length of northern anchovies older than 1½ yr: Central California (CC), San Nicolas (SN), Tanner-Cortez Banks (TCB), San Nicolas combined with Tanner-Cortez Banks (SN+TCB), Catalina Basin (CB), Santa Barbara Channel (SBC), Catalina Basin combined with Santa Barbara Channel (CB+SBC), San Pedro Channel (SPC), Coronado Escarpment (CE), Ensenada (E), Cape San Quentin (CSQ), Sebastian Viscaino Bay and Southern Baja California, central stock only (SVB+SB), and Southern Baja California, southern stock only (S).

Area	Mean age (Yr)	Mean length (SL mm)	Length at age 1½ (SL mm)	Adult growth (mm/yr)	*r*	SD of length at age 1½	SD of adult growth	*N*
				Central Stock				
CC	3.4	138.4	123.6	7.75	0.702	1.563	0.431	335
SN	3.3	131.1	120.4	5.97	0.613	0.713	0.205	1,410
TCB	3.2	130.8	119.2	6.69	0.623	0.975	0.286	860
SN+TCB	3.3	131.0	120.0	6.23	0.616	0.577	0.167	2,270
CB	3.1	126.7	116.4	6.29	0.582	0.633	0.192	2,092
SBC	2.9	125.6	116.2	6.83	0.636	0.689	0.224	1,374
CB+SBC	3.0	126.3	116.4	6.50	0.606	0.465	0.145	3,466
SPC	2.8	121.3	113.4	6.07	0.575	0.435	0.146	3,497
CE	2.7	118.7	110.5	6.89	0.569	0.666	0.235	1,798
E	2.8	116.5	106.2	8.08	0.636	0.944	0.321	934
CSQ	2.5	111.1	103.6	7.54	0.649	0.776	0.291	923
SVB+SB	2.4	106.4	101.1	5.76	0.443	1.571	0.618	358
				Southern Stock				
S[1]	2.9	91.9	91.8	0.07	0.009	1.274	0.421	335

[1]Combined from three areas: CSQ, SVB, and SB.

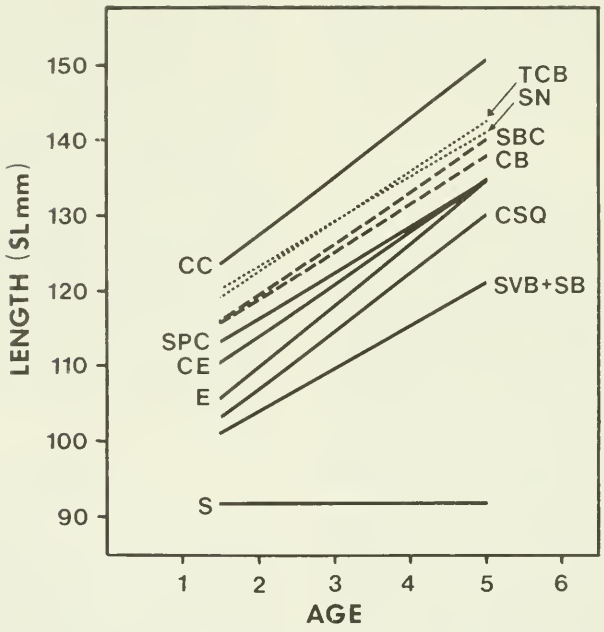

FIGURE 5.—Linear regressions showing the expected length at age (Table 1) of northern anchovies taken in CC, Central California; SN, San Nicolas; TCB, Tanner and Cortez Banks; CB, Catalina Basin; SBC, Santa Barbara Channel; SPC, San Pedro Channel; CE, Coronado Escarpment; E, Ensenada; CSQ, Cape San Quentin; SVB+SB, Sebastian Viscaino Bay and Southern Baja California, central stock only; and S, Southern Baja California, southern stock only.

patterns which are not statistically different (α = 0.01), and since the two regions are adjacent we have considered them together. Also there is no significant difference (α = 0.01) in adult growth in the Catalina Basin and the Santa Barbara Channel regions, but since these regions are geographically separated we have retained them as separate regions. The relatively large standard deviations of the regression slopes (Table 2) for fish from the Central California and the Sebastian Viscaino Bay and the Southern Baja California regions may indicate that these regions are the most likely to have mixtures of more than one stock.

There was no significant difference (α = 0.01) between growth of adults in the best growth regions (Ensenada, Cape San Quentin, and Central California). The difference between the Coronado Escarpment and the Santa Barbara Channel regions is not significant at the α = 0.1 level nor are the differences between the Catalina Basin, combined San Nicolas-Tanner and Cortez Banks, San Pedro Channel, and combined Sebastian Viscaino Bay and Southern Baja California regions.

Tanner and Cortez Banks, and Catalina Basin) differ from the other regions in that they are dominated by fish 3 yr and older (Fig. 6A, Table 4). Central California and Tanner and Cortez Banks also have substantial percentages of young-of-the-year fish, whereas the other two regions do not.

Anchovies in the three inshore regions of the Southern California Bight (Santa Barbara Channel, San Pedro Channel, and the Coronado Escarpment) have very similar age compositions (Fig. 6B, Table 4). One- and two-yr-old fish are the most numerous in these three regions. Young-of-the-year and 3 yr-olds are slightly less abundant than 1- and 2-yr-olds, and there are fewer older fish in the samples.

Baja California is characterized by a dominance of young fish (Fig. 6C, Table 4). The age compositions in the Ensenada, Cape San Quentin, and Sebastian Viscaino Bay regions are very similar; young-of-the-year and 1-yr-old fish are the most abundant, and there is rapid decrease in the abundance of fish with increasing age. Anchovies in southern Baja California are principally from the southern stock. The age composition in this region shows a predominance of 1-yr-olds, and like the other Baja California regions there are few fish of age 4 or older.

TABLE 3.—Significance levels for differences in growth of adult northern anchovies from different geographical regions: Ensenada (E), Central California (CC), Cape San Quentin (CSQ), Coronado Escarpment (CE), Santa Barbara Channel (SBC), Tanner and Cortez Banks (TCB), Catalina Basin (CB), San Nicolas combined with Tanner and Cortez Banks (SN+TCB), San Pedro Channel (SPC), San Nicolas (SN), Sebastian Viscaino Bay and Southern Baja California, central stock only (SVB+SB), and Southern Baja California, southern stock only (S). Geographic areas are arranged in order from largest to smallest slopes.

Area	E	CC	CSQ	CE	SBC	TCB	CB	SN+TCB	SPC	SN	SVB+SB	S
E	—											
CC	0.5573	—										
CSQ	0.2217	0.6517	—									
CE	0.0019	0.0514	0.0754	—								
SBC	0.0015	0.0477	0.0629	0.9422	—							
TCB	0.0013	0.0331	0.0384	0.6516	0.6951	—						
CB	0.0000	0.0000	0.0000	0.0605	0.0628	0.2400	—					
SN + TCB	0.0000	0.0003	0.0002	0.0283	0.0280	0.0000	0.8141	—				
SPC	0.0000	0.0000	0.0000	0.0015	0.0033	0.0465	0.3560	0.4659	—			
SN	0.0000	0.0000	0.0000	0.0042	0.0042	0.0367	0.2547	0.3234	0.6902	—		
SBV + SB	0.0000	0.0085	0.0051	0.0826	0.0952	0.1616	0.3943	0.4372	0.6048	0.7379	—	
S	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	—

Age Composition by Area

Geographical variation in age composition is one factor which could influence the observed variation in mean size of anchovies in the various regions; therefore, age composition was calculated for each of the regions used earlier (Fig. 2). Few anchovies < 60 mm SL occur in the data, and it appears that young-of-the-year fish are apparently not susceptible to capture by the midwater trawl gear used in the sea survey until they are about 6 mo old.

Central California and the three offshore regions within the Southern California Bight (San Nicolas,

Age Composition by Depth Strata

Anchovies primarily live within the upper mixed layer; they occur in the surface layer over the continental shelf and over deepwater regions. Mais (1974) showed that the average size of anchovies sampled in offshore areas was greater than that of anchovies sampled near the coast. The percentage of trawl hauls containing anchovies was quite constant in areas with different water depths, varying

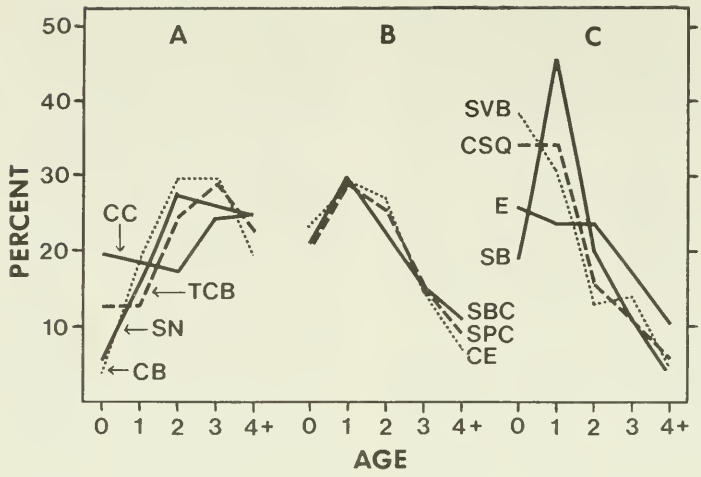

FIGURE 6.—Age composition of northern anchovies taken in the following geographical regions: A. Central California and offshore areas of the Southern California Bight; Central California (CC), San Nicolas (SN), Tanner and Cortez Banks (TCB), and Catalina Basin (CB); B. Inshore areas of the Southern California Bight; Santa Barbara Channel (SBC), San Pedro Channel (SPC), and Coronado Escarpment (CE); C. Baja California; Ensenada (E), Cape San Quentin (CSQ), Sebastian Viscaino Bay (SVB), and Southern Baja California (SB).

TABLE 4.—Percentage age composition of northern anchovies by geographical region: Central California (CC), San Nicolas (SN), Tanner-Cortez Banks (TCB), Catalina Basin (CB), Santa Barbara Channel (SBC), San Pedro Channel (SPC), Coronado Escarpment (CE), Ensenada (E), Cape San Quentin (CSQ) Sebastian Viscaino Bay (SVB), Southern Baja California (SB).

	Age							No.
Area	0	I	II	III	IV	V	VI+	fish
CC	19.3	17.2	14.7	23.9	17.7	5.7	1.6	436
SN	5.6	15.5	27.7	26.0	15.9	7.4	2.0	1,721
TCB	12.6	12.6	24.3	28.3	13.6	6.5	2.1	1,136
CB	3.7	18.7	29.2	29.2	12.8	5.2	1.1	2,538
SBC	21.8	29.6	22.2	15.2	8.2	2.4	0.6	1,989
SPC	21.6	28.6	25.4	15.6	6.3	1.9	0.5	5,439
CE	23.5	28.1	26.9	14.6	5.4	1.3	0.2	2,965
E	25.8	23.6	23.4	17.1	7.6	2.3	0.2	1,464
CSQ	33.8	33.7	15.5	11.2	4.4	1.2	0.1	1,779
SVB	38.1	30.8	12.8	13.5	4.5	0.3	—	896
SB	18.8	45.7	19.6	11.5	3.7	0.7	—	409

between 64 and 77% (Table 5). This is probably influenced by the fact that trawling (in the upper 30 m) was carried out normally in areas where fish schools had already been detected by depth recorder or sonar.

In southern California (lat. 32°-34°N) young-of-the-year anchovies comprise more than one-half of the anchovies sampled in the 5-25 fathom-depth stratum (Table 6A). One- and two-yr-olds comprise more than one-half of the anchovies in the 26-50, 51-150, 151-300, and 301-500 fathom strata. The most abundant age group in the 26-50 stratum is age 1; there are essentially equal numbers of age 1 and age 2 anchovies in the 51-150 and 151-300 strata; 2-yr-olds are the most abundant age group in the 301-500 stratum; and 3-yr-olds are the most abundant age group in the 701+ stratum. Age groups 3-6+ each show an increasing percentage with increasing depth. Collectively they comprise about 11% of the 5-25 stratum, 31% of the 51-150 stratum, and 51% of the 701+ stratum. The same general pattern occurs in northern Baja California (lat. 29.5°-32°N); however, the percentage of young fish declines more

TABLE 5.—Percentage of midwater trawl hauls taking northern anchovies by depth strata. Trawl hauls were normally within 30 meters of the surface.

Depth (fm)	Total sets	% sets with anchovies
5-25	704	75
26-50	828	69
51-150	554	69
151-300	546	76
301-500	752	77
501-700	437	73
701+	345	64
Total	4,166	72

TABLE 6.—Age composition (%) of northern anchovies taken in shallow and deep-water areas (depth in fathoms).

A

		Lat. 32°-34°N						
Age	Depth:	5-25	26-50	51-150	151-300	301-500	501-700	701 +
0		56.5	26.3	16.9	7.8	5.5	3.0	6.5
I		20.6	29.5	26.5	27.4	25.8	17.9	15.5
II		12.5	24.1	26.0	27.9	30.6	32.0	26.8
III		7.0	12.3	20.1	22.8	22.7	28.2	27.1
IV		2.5	5.8	6.8	9.1	10.5	13.3	15.3
V		0.8	1.5	3.2	3.6	3.8	4.9	7.2
VI +		0.2	0.5	0.6	1.4	1.1	0.6	1.7
n		1,579	1,492	1,102	2,199	3,704	2,091	1,086

B

		Lat. 29.5°-32°N			
Age	Depth:	5-25	26-50	51-150	151 +
0		56.1	36.8	21.0	8.9
I		23.1	40.4	28.5	28.8
II		12.3	10.8	24.2	26.9
III		6.2	7.8	14.2	23.3
IV		1.9	3.6	9.4	8.7
V		0.3	0.6	2.5	3.0
VI +		—	—	0.2	0.3
n		935	619	480	1,189

C Aug.-Dec.

		Lat. 29.5°-32°N				Lat. 32°-34°N			
Age	Depth:	5-25	26-50	51-150	151 +	5-25	26-50	51-150	151-300
0		62.8	52.6	38.7	24.9	66.2	37.8	26.4	16.0
I		18.2	32.3	29.2	43.0	15.6	29.0	24.7	21.0
II		11.7	10.6	19.9	24.4	12.1	22.5	25.8	32.4
III		5.7	4.0	8.2	6.4	5.0	8.6	16.1	21.2
IV		1.6	0.5	4.1	1.2	0.9	2.0	5.1	8.3
V		—	—	0.7	—	0.2	0.1	1.8	0.9
VI +		—	—	—	—	—	—	—	0.2
n		806	378	267	405	1,286	1,013	546	990

slowly with increasing depth there than in southern California (Table 6B). In both southern California and northern Baja California, there is a direct relationship between average age and depth of water in which fish were caught. In the period August-December when smaller (< 60 mm) anchovies can be caught by midwater trawls, there is a greater dominance of young-of-the-year fish in the shallower water (Table 6C). In the northern Baja California area, 63% of the 5-25 stratum and 53% of the 25-50 stratum were young-of-the-year fish. In southern California the corresponding percentages were 66 and 38.

Sea Survey - Fishery Comparisons

The purse seine fleets which harvest anchovies operate primarily out of San Pedro, California, and Ensenada, Mexico. The age composition of anchovies in the San Pedro fishery (Mallicoate and Parrish 1981) contains a smaller proportion of age 0 and age 1 fish than does the sea survey data for the San Pedro Channel region. We only had 2 years of age composition data for the Ensenada fishery available to us (Sunada and Silva 1980), but this limited information shows the same dominance of younger anchovies as in the sea survey data for this region. The San Pedro fishery had several regulations which reduced the numbers of young fish in the catch. These included a 5-in minimum size limit and a series of area closures which prevent the fleet from fishing in nearshore areas. The Ensenada fishery did not have regulations which influenced the age composition of the catch.

To evaluate the effects of the area closures and size limit on the San Pedro fishery, we broke the sea survey data into depth classifications, < 50 fathoms and > 50 fathoms. The > 50 fathom classification was intended to approximate the area of the fishery (i.e., the coastal strip is excluded). In this area the

age composition of anchovies taken by the Sea Survey Program is very close to that taken by the fishery; conversely, the age composition of the fishery is unlike that taken in areas < 50 fathoms (Fig. 7). The California fishery no longer has a 5-in size limit; however, the closure of the nearshore area appears to be the dominant factor in reducing the catch of young anchovies.

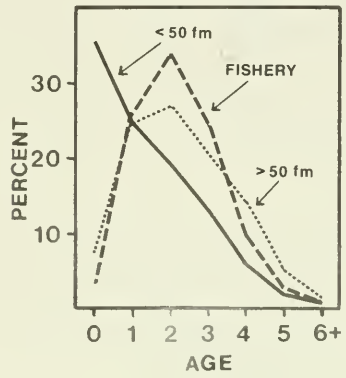

FIGURE 7.—Comparison of the age composition of northern anchovies taken in the San Pedro purse seine fishery with those taken in areas with <50 fathoms and >50 fathoms of water in the midwater trawl Sea Survey Program.

DISCUSSION

Our data show that the growth rate and the age composition of northern anchovies vary geographically. The greatest differences in growth appear to occur during the juvenile stage; growth in adults shows much less regional variation. Juvenile growth is greatest in central California and in the offshore areas of the Southern California Bight. In the inshore regions there is a trend toward reduced juvenile growth from central California to southern Baja California. Average size at age 1½ falls from 123.6 mm to 91.8 mm over this area. Growth in adult anchovies appears to be the greatest in northern California, and it is also relatively high in British Columbia (Pike 1951), central California, and northern Baja California. Adult growth appears to be relatively low in the Southern California Bight; this, however, may be an artifact as this area probably includes resident fish plus slower growing fish which have moved into this region from the south. Age composition showed a large variation among regions, and the pattern of this variation appears to be closely related to the gyral circulation within the Southern California Bight. There is also a strong relationship in age composition to the depth of water at trawl sites. Adult anchovies dominated the catches in the offshore, deepwater regions of the Southern California Bight and in central California. Age also had a strong latitudinal gradient with adult fish dominating in the north and young-of-the-year and yearling fish dominating in the shallow water areas off central and northern Baja California. Adult anchovies appear to be concentrated in areas of the Bight where prevailing currents will result in southerly and inshore larval transport (Parrish et al. 1981). At recruitment, anchovies appear to be heavily concentrated in shallow water, and young fish appear to be concentrated in the nearshore area where they will tend to be advected northward by the southern California gyre.

As will be discussed later, the interpretation of the regional differences in juvenile growth is dependent upon the stock structure in the various regions. Earlier studies (McHugh 1951; Vrooman et al. 1981) showed that the boundary between the southern and central stocks was in the northern Sebastian Viscaino Bay area. This is supported by the present study, and, as previously mentioned, the boundary is further north in the summer and fall and further south in winter and spring. We feel that there is ample evidence that the southern stock had the smallest juvenile growth rate and that growth during the adult phase is minor. Vrooman et al. (1981) suggested that the boundary between the northern and central stocks occurs in the central California area; both northern and central stocks occurred in samples taken at San Francisco (lat. 37°50′N) and Monterey (lat. 36°50′N). Their data might be interpreted to suggest that a fourth stock occurred in the San Francisco and Monterey samples, and in addition it has been suggested (Parrish footnote 3) that this fourth stock spawns during the fall in central California and the offshore areas of the Southern California Bight. Unfortunately the Vrooman et al. (1981) study did not have any samples from the region between Monterey (lat. 36°50′N) and Newport (lat. 33°30′N), nor were there any samples from the offshore areas of the Southern California Bight. It is therefore not presently possible to determine the amount of stock mixture over much of the accepted range of the central stock.

Variation in juvenile growth of northern anchovies in the different regions may be due to genetic factors, differences in the seasonality of spawning, or environmental factors. The northern stock has a relatively short spawning season with a strong peak in July (Richardson 1980). The central stock has a

more extended spawning season with a broad peak from February to April, and there is some spawning all year in the central stock region. It is not yet known if the anchovies that spawn in central and southern California during the summer and fall are from the central stock, northern stock, or a possible fall spawning stock. If the anchovies in this region are predominatly from the central stock, the relatively high juvenile growth in central California and the offshore portion of the Bight might be due to a favorable feeding environment. Offshore portions of the Southern California Bight have been shown to have considerably more plankton and nutrients than the inshore portions (Reid et al. 1958; Owen 1980). If the anchovies in the area occupied by the central stock have a large component that are not central stock, the increased juvenile growth could be due to the genetic differences, due to environmental differences, or caused by the assumption of a February birth month. At our "assumed" age of 1½ yr, an anchovy spawned in the fall would be about 6 mo older than the "normal" central stock anchovy. If the growth that occurred during these additional 5 mo was at the normal adult rate (i.e., 0.48-0.69 mm/mo), there would be only a 2-4 mm difference in the size of the two fish. However, the difference in mean length between 1½-yr-old anchovies in the central California and Cape San Quentin regions is 20 mm. If, however, growth during the 5 mo is even one-half of the average juvenile rate (i.e., 9 mm/mo) the difference in size at "1½" yr could be achieved.

CONCLUSION

The interpretation of regional variations in the growth and age composition of northern anchovies in the area between central California and central Baja California and the implications of this study for fisheries management are dependent upon the stock structure of the anchovies in the area.

If a significant proportion of these fish are not from the central stock, this study suggests the following:

1. The observed regional variation in age composition may be the result of mixtures of stocks with different mortality rates.
2. The juvenile growth rate of anchovies in the central stock is lower than that of anchovies from the northern stock(s). The reason for this lower growth rate could be either genetic, environmental, or dependent upon the seasonality of spawning.
3. The southern California and Mexican fisheries are based on different stock mixtures, and thus the interactions between these fisheries would not be as great as they would be if both were based entirely on the same stock.

If essentially all of these anchovies are from the central stock, this study suggests the following:

1. The offshore regions of the Southern California Bight contain a disproportionate share of the adult anchovies; however, recruitment does not occur here to any significant extent.
2. Recruitment occurs largely in shallow water along the coast, and the northern Baja California region has the largest percentage share of young-of-the-year anchovies.
3. Larvae and juveniles recruited from the offshore regions of the Southern California Bight tend to move or be advected south and inshore.
4. The relatively high juvenile growth rates in central California and the offshore regions of the Southern California Bight are due to favorable environmental conditions.
5. As they grow older anchovies tend to move, or be advected, north and offshore.
6. Mixing of adults is not complete; otherwise length at age and age composition would be the same everywhere.
7. Due to the inferred tendency for recruitment to occur in the south, an extensive fishery on the central stock would reduce the proportion of older anchovies and result in fewer older anchovies in the northern and offshore areas.
8. The combination of the large Mexican fishery, which has been associated with a reduction in the proportion of older anchovies (Mais 1982), and the continued closure of the nearshore areas where younger fish are concentrated will severely impact the California fishery.

ACKNOWLEDGMENTS

We are grateful to Roy Mendelssohn, Alec MacCall, Janet Mason, and Rick Methot for their comments and editorial assistance. In addition we wish to thank Susie Myers for her help in completing the manuscript.

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PARASITES OF BENTHIC AMPHIPODS: MICROSPORIDANS OF *AMPELISCA AGASSIZI* (JUDD) AND SOME OTHER GAMMARIDEANS

PHYLLIS T. JOHNSON[1]

ABSTRACT

Microsporidan infections were found in individuals of 11 species of benthic amphipods collected during a 2½-year survey of populations on the continental shelf of the northeastern United States. *Ampelisca agassizi* (Judd) was the most numerous and broadly distributed species of amphipod. A microsporidan confined to the abdominal muscles was common in most populations of *A. agassizi*. It is provisionally assigned to the genus *Thelohania*. There were prevalences up to 37% depending upon the population surveyed, but the microsporidans did not seem to contribute to mortality in *A. agassizi* populations, with the possible exception of adult males. Microsporidans in other amphipod species parasitized various organs and tissues according to the amphipod species and type of microsporidan. The relationships of the microsporidans with the genera *Thelohania*, *Stempellia*, and *Nosema* are discussed.

In the late 1970's, a monitoring program was developed within the National Oceanic and Atmospheric Administration (NOAA) to assess the presence of pollutants and their effects on the fauna and flora of the continental shelf of the United States. As a part of this plan, the Northeast Monitoring Program (NEMP) has been conducted on a seasonal basis from the Gulf of Maine to Cape Hatteras by the Northeast Fisheries Center, National Marine Fisheries Service. In connection with NEMP, studies have been made of types and prevalences of parasites, diseases, and other abnormalities of various populations of benthic gammaridean amphipods. Samples were mainly from stations on the Georges Bank and Mid-Atlantic Bight.

The results of the survey will be presented in a series of papers. This, the first report, discusses microsporidan parasites, particularly those of *Ampelisca agassizi* (Judd).

Published information on parasites and pathological conditions of gammaridean amphipods is limited and concerns mainly the parasites of selected estuarine and freshwater species, particularly the microsporidan parasites (Bulnheim 1975). Data collected during the present survey concern a broad array of species of marine amphipods. Communities of benthic amphipods are unlike most animal communities because they are composed of numerous individuals of several to many related species that live in very close proximity to one another. Indeed, it is common for a population to contain two or more species of a single genus. It is also common for a thousand or more individuals of a single species, together with varying numbers of other species, to be crowded onto one-tenth of a square meter of the bottom (Dickinson et al. 1980). This unique population structure makes studies of parasites and diseases of the amphipods of great general biological interest.

The methods used for collecting and preparing the benthic amphipods are satisfactory for study of many facets of the host-parasite relationships that exist in these animal communities: effects of parasites on their hosts, host specificity of parasites, seasonal prevalence, and modes of passage of parasites through host populations. On the other hand, paraffin-embedded sections seldom allow specific identification of parasites. Depending on the parasite group, this may require examination of live animals or of whole specimens fixed and stained by special methods.

It is hoped that the data presented here and elsewhere will serve as a framework for more definitive studies on the taxonomy, life history, and other aspects of the various parasite species.

MATERIALS AND METHODS

Amphipods were sampled 11 times over a 2½-yr period from July 1980 to December 1982 on NEMP cruises (Table 1). The 35 stations where benthic amphipods were collected are shown in Figure 1. Not all stations were visited on each cruise, being sampled from 1 to 10 times each during the survey. The 11 stations indicated by solid circles on Figure 1 had

[1]Northeast Fisheries Center, Oxford Laboratory, National Marine Fisheries Service, NOAA, Oxford, MD 21654.

Manuscript accepted November 1984.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985

TABLE 1.—Sampling cruises for benthic amphipods, July 1980-December 1982.

Date	NEMP cruise no.	Cruise designation
July 1980	AL80-07	A
September 1980	AL80-09	B
December 1980	DE80-09	C
April-May 1981	KE81-04	D
July 1981	AL81-07	E
August-September 1981	AL81-10	F
November 1981	DE81-07	G
January-February 1982	AL82-01	H
March-April 1982	AL82-03	I
August-September 1982	AL82-10	J
November-December 1982	AL82-12	K

consistent, and usually numerous, amphipod populations and were sampled five or more times. They yielded the majority of data presented in this paper.

Collections of bottom sediments and accompanying biota were made with a 0.1 m^2 Smith-McIntyre[2] grab. Generally a single grab was taken at each station sampled. If the first grab contained few amphipods but was from a station where they usually were abundant, a second and sometimes a third grab was taken. Sediment contained in the grab was washed through a 1.0 mm sieve, and amphipods were either collected with forceps or gently scraped from the sieve and placed in a jar of 10% seawater Formalin. On cruises A, B, and E (see Table 1), supplemental specimens were collected at some stations by use of an epibenthic sled or scallop dredge.

Storage of samples was in Formalin except that amphipods were transferred temporarily into 30 ppt artificial seawater for identification and enumeration, inspection for various gross lesions, and for determination of life-history stages and microsporidan infections of the muscle in the case of *Ampelisca agassizi* (Judd). A stereomicroscope was used for these procedures. Up to 30 and occasionally more individuals of each species in the sample, depending on numbers present, were processed for histological examination by standard means. Finished tissue sections were stained with hematoxylin and eosin. Depending on size and number to be embedded, 1 to 12 amphipods of a single species from a single station were embedded on their sides in each paraffin block. Several serial sagittal sections were taken, first laterally and then near the midline of the amphipods. Because of unavoidable variations in size and depth of the amphipods in the block, not all were sectioned at the same levels. Parts of the hemocoel, skeletal muscle, and appendages of all amphipods were present in sections. Usually, parts of the gills, hepatopancreas and other parts of the gut, heart, brain, and gonads were also present. Other tissues and organs, particularly the antennal gland, hemopoietic tissues, eyes, and ventral nerve cord, often were not included.

Measurements of microsporidan spores were based on fixed material, either whole or embedded, sectioned, and stained.

RESULTS

The amphipod population sampled at any one time at a particular station was a mixture of up to 14 different species. Commonly five to eight species were collected in a single grab except at station 23, which was strongly dominated by *Ampelisca agassizi*. Of eight samples from station 23, three contained only *A. agassizi*, and *A. agassizi* made up 94 to 99% of the remaining samples. Totals of the eight samples from station 23 were 2,788 individuals of *A. agassizi* and 23 individuals of other species (99% *A. agassizi*).

Ampelisca agassizi was the most numerous and broadly distributed of the species investigated, and occurred at 17 stations including the 11 major ones. Certain information on the life history of this species is pertinent. It is an annual, tube-building species that produces a single brood of young (Bousfield 1973). Overwintering is in the juvenile stage. Gonads of both sexes develop during the subadult stage. Breeding begins in the spring, and newly ovigerous females are found from spring through autumn. Postovigerous females tend to remain in the population for an unknown period after the young are released from the brood pouch. Adult males are pelagic or epibenthic, probably short-lived, and usually were missing from samples collected with the Smith-McIntyre grab. Only the adult male has strongly developed transverse pleosomal muscles (muscles of the first three abdominal segments) (Fig. 2). Presumably, these muscles aid in swimming. The transverse muscles lie lateral to the longitudinal muscles and are developed during the subadult stage. They can be seen in various stages of development through the translucent cuticle of subadult males.

Females of the gammaridean, tube-dwelling amphipods so far studied leave their tubes to molt to the adult stage. Mating and egg extrusion take place in the water column (Mills 1967). Population dispersal is presumed to occur either by ovigerous females settling away from their original location

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

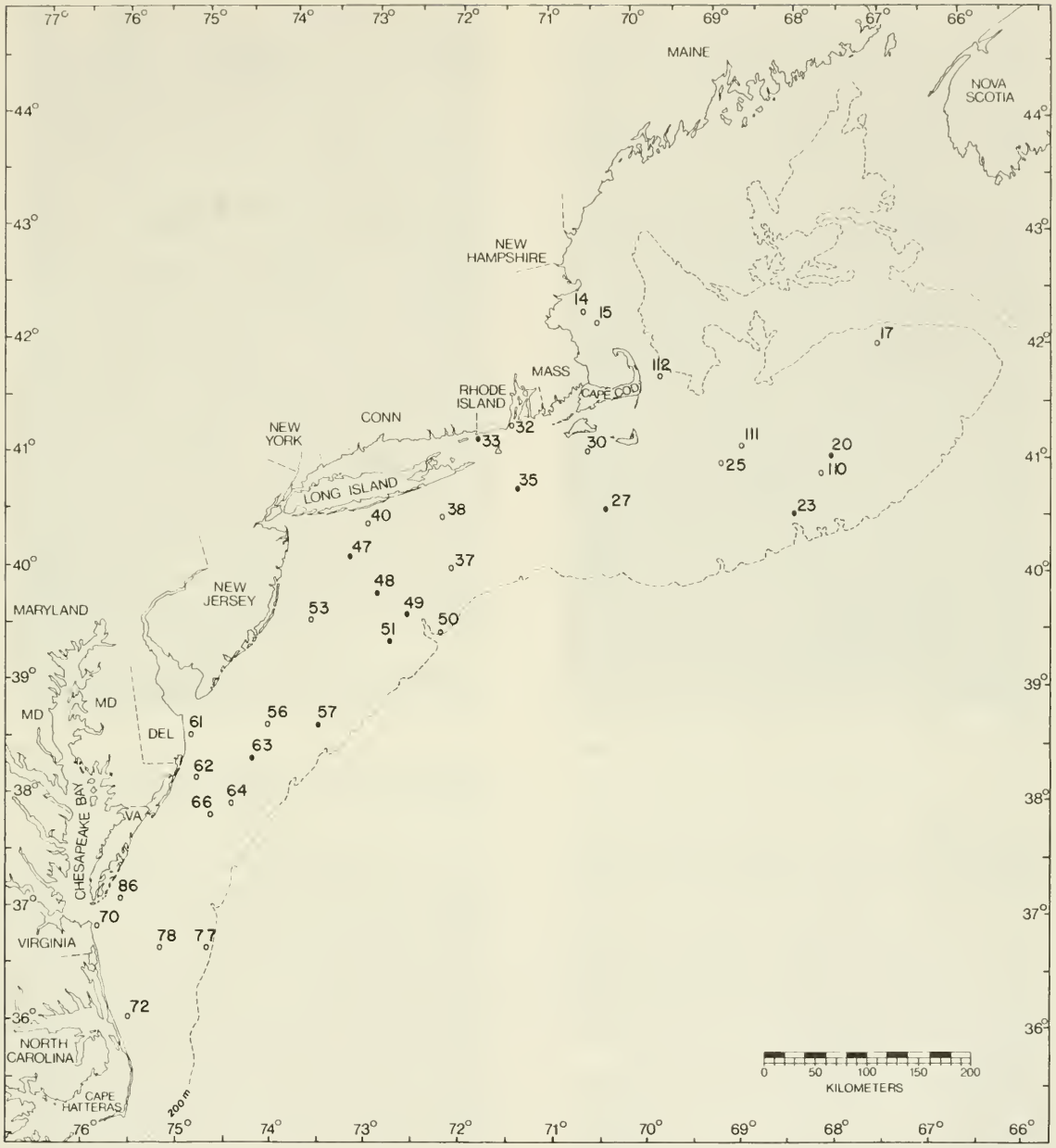

FIGURE 1.—Benthic stations of Northeast Monitoring Program at which populations of gammaridean amphipods were sampled during the survey, 1980-82.

and probably in a less populated area (Mills 1967) or by emigrating juveniles (Bousfield 1973). Thus, juveniles and perhaps ovigerous and postovigerous females of *A. agassizi* and other species could at times be immigrants into locations with already established populations of older juveniles and subadult males and females.

Microsporidans of *Ampelisca agassizi*

Most of the populations of *A. agassizi* sampled were regularly infected by a species of microsporidan that attacks the longitudinal pleosomal muscles (Figs. 3, 4). Infected muscles were chalky white in fully developed infection, and easily visible through

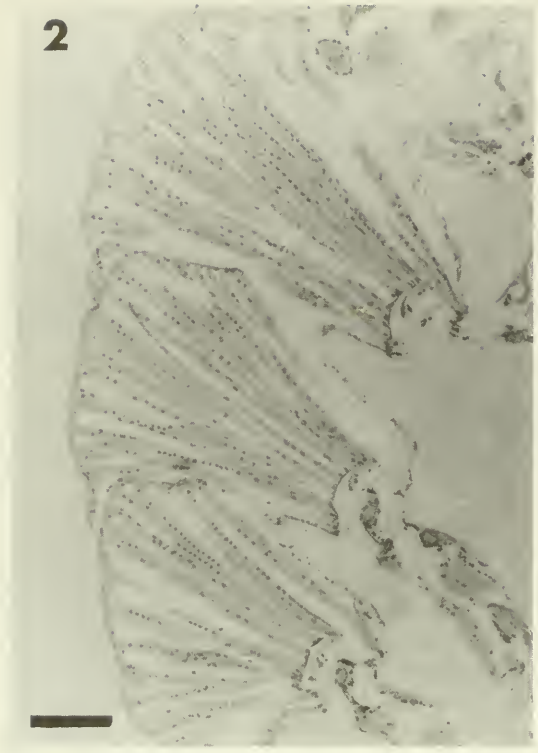

FIGURE 2.—*Ampelisca agassizi*: Transverse pleosomal muscles of an adult male. Bar = 0.2 mm.

FIGURE 3.—*Ampelisca agassizi*: Longitudinal pleosomal muscles infected by microsporidans (open arrows). Normal muscle is also present (closed arrow). g, midgut. Bar = 0.2 mm.

the translucent cuticle. Usually, only one to three muscles were infected. Inspection of 150 microsporidan-infected amphipods showed that in eight cases transverse pleosomal muscles were also involved, and in three cases, only the transverse muscles were infected. One postovigerous female, with microsporidan infection in muscle, also had what appeared to be the same organism in one of the ganglia of the ventral nerve cord.

On the basis of a tissue section she examined, A. Cali[3] determined that this microsporidan is a pansporoblastic organism with the clusters appearing to be in groups of eight. However, she said further that possibly some clusters contained more than eight spores. This is a point difficult to determine in sectioned material. Spores are oval and of fairly uniform size. Ones dissected out singly from infected muscle (not paraffin embedded) measured approximately 3 μm × 1.5 μm. In Cali's opinion, the *A. agassizi* parasite is best provisionally placed in the genus *Thelohania*, without specific designation.

[3]A. Cali, Rutgers University, Newark, NJ 07102, pers. commun. 1983.

Numerical information on this microsporidan is based on samples taken on cruises D-K, because determination of microsporidan infection was by study of sectioned material only from cruises A-C, and infections can be missed by this method. Considering all stations on cruises D-K, juveniles had a lower prevalence of grossly visible infection than did male and female subadults and ovigerous females (Table 2), but this was not invariably the case in individual samples. In 5 of the 38 samples with micro-

TABLE 2.—Prevalence of microsporidan infections in *Ampelisca agassizi* by life-history stages. All stations, cruises D-K.

Life-history stage	No. infections/ total collected (% prevalence)
Juveniles	517/4,868 (11)
Subadults	1,335/5,293 (25)
Ovigerous females	111/501 (22)
Postovigerous females	82/413 (20)
Adult males	1/55 (2)
Totals	2,046/11,130 (18)

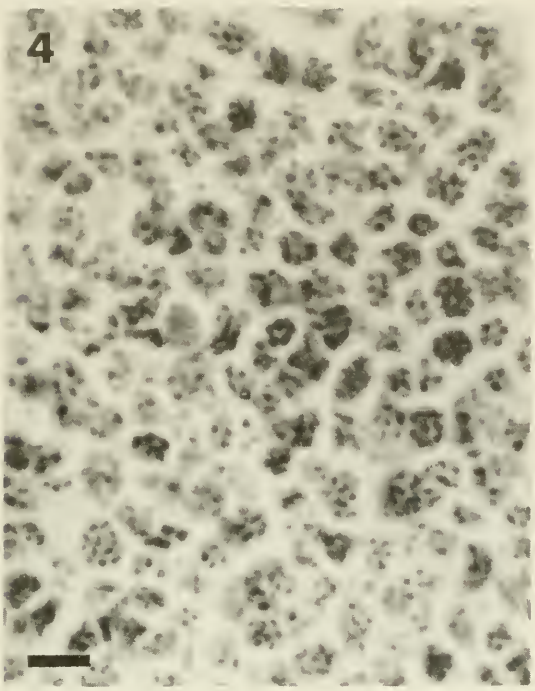

FIGURE 4.—*Ampelisca agassizi*: Groups of spores and prespores of the muscle-infecting microsporidan. Bar = 10 μm.

sporidan-infected *A. agassizi*, prevalence was equal to or slightly higher in juveniles than in subadults or ovigerous females. Prevalence was very low in the small sample of adult males, but varied considerably in individual samples of both males and postovigerous females (Table 3). The three stations with the most consistently numerous populations of *A. agassizi* also had the highest prevalences of microsporidan infection. These were stations 23, 33, and 48, with overall prevalences of 30%, 37%, and 22%, respectively. Overall prevalence at other stations ranged from 0 to 14%.

The majority of infected hosts showed no reaction to the presence of the microsporidans. However, there was occasional melanization in heavily infected muscle, with invasion of hemocytes into the mass of spores, some encapsulation of spores and infected muscle, and lysis of many spores. In these cases, it appeared that the muscle had lost its integrity; that is, the sarcolemma probably was no longer entire. Often, other infected muscle near the necrotic mass of spores and muscle showed no evidence of attack by host defense mechanisms.

The second microsporidan of *A. agassizi* parasitized epithelial cells of the posterior half of the midgut. Juveniles, male and female subadults, and ovigerous and postovigerous females were infected. The parasite resembled *Nosema*, the spores being single and free in the cytoplasm of the host cell (Fig. 5). Spores were slightly oval and about 2 μm in the greater dimension. Infected cells were hypertrophied (Fig. 6). In one heavy infection, many spores were free in the gut and apparently most infected cells had ruptured. There was no host reaction to infection. This parasite occurred twice in individuals with microsporidan infection in abdominal muscle. Based on sectioned material, overall prevalence of the gut microsporidan was < 0.1% (25/2403). Prevalence in samples with one or more infected *A. agassizi* was 3.7% (25/678), range 1-6%. Amphipods with microsporidans in the gut epithelium were from stations 23, 33, 47, 48, 49, 50, and 51.

Microsporidans in Species Other Than *A. agassizi*

Males and females of *Unciola* species (probably all *U. irrorata* Say and *U. inermis* Shoemaker) were hosts to a microsporidan that infected longitudinal muscles of the pleosome. In three instances, a similar or the same microsporidan was found in a ganglion of the ventral nerve cord, and not in muscle. Spores appeared similar to those of the *A. agassizi* parasite; they measured about 3 × 1.5 μm; and there were eight or more spores per envelope. Unlike the *A. agassizi* parasite, vegetative stages were often present along with developed and developing spores. *Unciola* species have an opaque cuticle, and infected muscle cannot be seen grossly. Based on sectioned

TABLE 3.—Prevalence of microsporidan infections in *Ampelisca agassizi* by life-history stages. Stations 47 and 48, cruises E and F.

Life-history stage	No. infections/ total collected (% prevalence)	No. infections/ total collected (% prevalence)
	Cruise E	Cruise F
Station 47	(depth 48 m)	(depth 62 m)
Juveniles	29/851 (3)	130/1,124 (12)
Subadults	45/258 (17)	12/53 (23)
Ovigerous females	14/84 (17)	11/53 (20)
Postovigerous females	0/24 (0)	6/29 (21)
Adult males	0/34 (0)	1/3 (33)
Totals	88/1,251 (7)	160/1,262 (13)
	Cruise E	Cruise F
Station 48	(depth 72 m)	(depth 68 m)
Juveniles	2/33 (6)	5/29 (17)
Subadults	66/246 (27)	28/111 (25)
Ovigerous females	0 (—)	11/51 (22)
Postovigerous females	0 (—)	3/27 (11)
Adult males	0/1 (0)	0/4 (0)
Totals	68/280 (24)	47/222 (21)

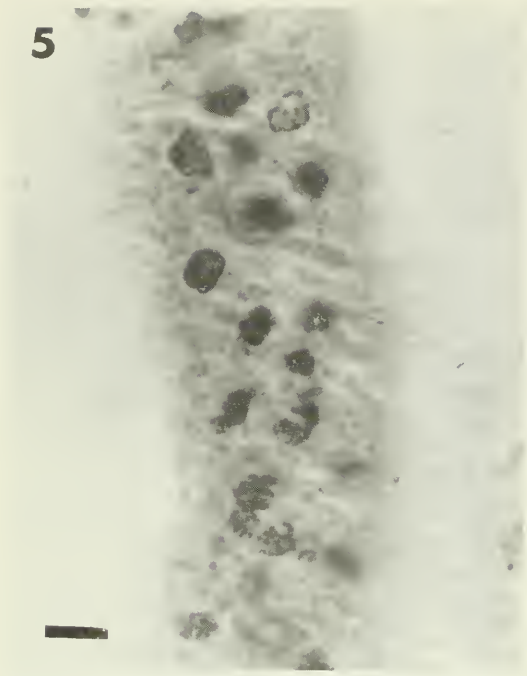

FIGURE 5.—*Ampelisca agassizi*: *Nosema*-like microsporidan in the midgut epithelium. Bar = 10 μm.

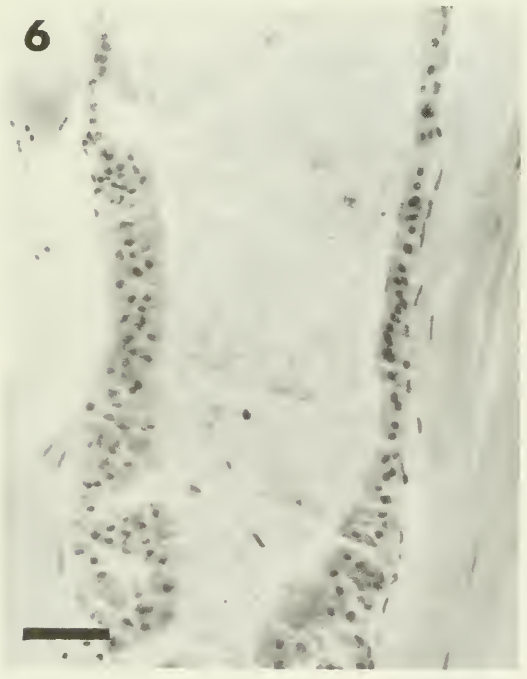

FIGURE 6.—*Ampelisca agassizi*: Hypertrophy of midgut epithelial cells infected by a *Nosema*-like microsporidan. Infected epithelium to left, normal epithelium to right. Bar = 60 μm.

material, prevalence was 8.3% (23/277), considering only samples containing infected *Unciola* spp. Prevalence was 1.7% when considering all *Unciola* spp. that were sectioned and examined (Table 4). There was no host reaction to infection in the ganglia, but animals with muscle infection often showed some melanization and encapsulative response (Fig. 7). Scattered small melanized nodules were common in the hemocoel of infected *Unciola* spp., but it was not evident whether they had formed in response to microsporidans.

Other amphipod species with microsporidan infections are listed in Table 4. Prevalence was usually very low. Most of the parasites appeared like the muscle-infecting microsporidans of *A. agassizi* and *Unciola* spp. A *Nosema*-like parasite similar to the gut microsporidan of *A. agassizi*, but smaller (0.7 μm), occurred in the hepatopancreatic epithelium of a specimen of *Leptocheirus pinguis* (Stimpson). Another *L. pinguis* harbored a larger *Nosema*-like species in oocytes and heart muscle. Infected oocytes were necrotic and encapsulated by hemocytes. The generalized muscle parasite of *Melita dentata* (Krøyer) *s. lat.* was also *Nosema*-like.

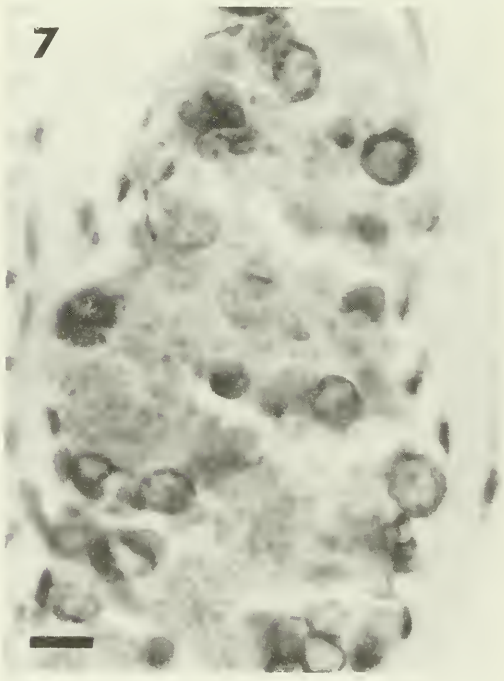

FIGURE 7.—*Unciola* sp.: Host reaction to microsporidans in abdominal muscle. Some groups of degenerating spores and prespores are surrounded by melanized material. A few nuclei of encapsulating host cells are visible around the mass of microsporidans. Bar = 10 μm.

TABLE 4.—Microsporidans in amphipods other than *Ampelisca agassizi*.

Amphipod species	No. infections/ total examined (% prevalence)	Positive stations	Tissues infected	Type of microsporidan
Unciola spp. (*irrorata* Say and *inermis* Shoemaker)	23/1,365 (1.7)	33, 35, 38, 47, 48, 51, 110, 112	Abdominal muscle, ganglia of ventral nerve cord	"*Thelohania*"
Ampelisca vadorum Mills	4/448 (0.9)	57, 66	Muscle, tegmental glands, oocytes	"*Thelohania*"
Ampelisca verrilli Mills	1/48 (2.1)	62	Connective tissue, muscle	"*Thelohania*"
Ericthonius rubricornis Smith	1/436 (0.2)	38	Abdominal muscle	"*Thelohania*"
Eriopisa elongata (Bruzelius)	1/29 (3.4)	47	Ganglia of ventral nerve cord	"*Thelohania*"
Leptocheirus pinguis (Stimpson)	1/913 (0.1)	47	Abdominal muscle	"*Thelohania*"
	1/913 (0.1)	15	Oocytes, heart muscle	*Nosema*-like
	1/913 (0.1)	20	Epithelium of hepatopancreas	*Nosema*-like
Melita dentata (Krøyer) *s. lat.*	2/44 (4.5)	51	Generalized in muscle	*Nosema*-like
Monoculodes edwardsi Holmes	1/110 (0.9)	40	Abdominal muscle	"*Thelohania*"
Photis dentata Shoemaker	4/301 (1.3)	33	Abdominal muscle, ganglia of ventral nerve cord	"*Thelohania*"

The microsporidan of *Ampelisca vadorum* Mills resembled that of *Unciola* spp., but fully developed spores were not seen (Fig. 8). Muscle, tegmental glands, and oocytes were infected. Often, groups of microsporidans had "used up" the host tissue, and appeared like groups of extracellular, closely knit, vegetative and sporulating stages, but some of these groups were unmistakably in the shape of tegmental glands and oocytes and were in the correct anatomical positions. In one case, muscle fibers were still present adjacent to the mass of microsporidans and in another, microsporidans infected a recognizable tegmental gland. Host reactions to the microsporidans had not occurred in the few infected *A. vadorum* available for study.

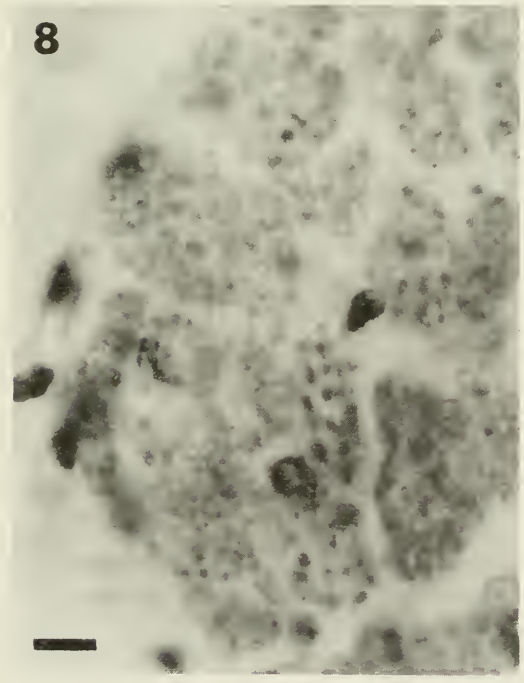

FIGURE 8.—*Ampelisca vadorum*: Vegetative and prespore stages of a muscle-infecting microsporidan. Bar = 10 μm

More than 35 specimens each of the following species were sectioned and examined, but microsporidans were not found: *Anonyx sarsi* Steel & Brunel (36 specimens), *Byblis serrata* Smith (316 specimens), *Casco bigelowi* (Blake) (60 specimens), *Corophium crassicorne* (Bruzelius) (50 specimens), *Harpinia propinqua* Sars (116 specimens), *Orchomenella minuta* Krøyer (64 specimens), *Phoxocephalus holbolli* Krøyer (73 specimens), *Pseudunicola obliquua* (Shoemaker) (46 specimens), and *Rhepoxynius epistomus* (Shoemaker) (249 specimens).

DISCUSSION

Bulnheim (1975) and Sprague (1977) have listed and discussed the various microsporidans reported from amphipods. Most of the hosts are freshwater and estuarine forms, and depending on the species

of microsporidan, muscles, ovaries, connective tissues, and gut epithelia are infected. One of the microsporidans, a parasite of *Gammarus pulex* L., infects the longitudinal abdominal muscles of its host in the same manner as does the *A. agassizi* parasite, but is known to have a variable number of spores per envelope. It was named *Glugea muelleri* (Pfeiffer, 1895, in van Ryckeghem 1930), later named *Thelohania giraudi* (Léger and Hesse, 1917), and has been called *Stempellia muelleri* (Pfeiffer) by Bulnheim (1975) and *Microsporidium giraudi* (Léger and Hesse) by Sprague (1977). The relationship of "*Glugea muelleri* Pfeiffer" and the microsporidan from *A. agassizi* remains to be determined. Although "*Glugea muelleri* Pfeiffer" and the *A. agassizi* parasite are remarkably similar in being restricted to the longitudinal abdominal muscles of their hosts, the latter is probably significantly smaller. Fixed spores of the *A. agassizi* parasite are about 1.5 × 3 μm, and fresh spores of "*Glugea muelleri*" are 2.2 × 4.5 μm.

The method of transmission of the *A. agassizi* parasite is not known. Microsporidans are usually transmitted orally, but transovarial transmission also occurs in amphipods. Transovarially transmitted microsporidans of *Gammarus duebeni* Lilljeborg infect the ovary, and, depending on the species, cause complete or partial feminization of males (Bulnheim 1975, 1977). The parasite of *A. agassizi* did not infect the ovary, and because it was regularly found in normal males, it apparently does not cause feminization of males. Bulnheim (1971) successfully transmitted "*G. muelleri* Pfeiffer" to several species of *Gammarus*, including euryhaline ones, by feeding of infected muscle.

Prevalence of the muscle parasite of *A. agassizi* apparently increases with age of the host, and it could be hypothesized that this microsporidan is transmitted orally, that the older the host the more chances it has had to become infected, and that the parasite does not contribute to increased mortality in the population. Adult males are active swimmers and might prove an exception because impaired muscle function could lead to increased predation. If this occurred, one would expect infected males to be preferentially removed from the population, leading to a lower prevalence of infection in this stage. Indeed, prevalence in adult males was only 2%. However, relatively few males were collected during the survey, and the low prevalence could prove to be sampling artifact. Note that in the sample from cruise E, station 47 (Table 3), both postovigerous females and adult males were uninfected, but 2 mo later, at the same station, prevalence in postovigerous females was 21% and the only infected adult male found during the survey was also collected at that time. The discrepancy in prevalence might be due to sampling of slightly different populations. As discussed below, there is no assurance that the same population was sampled spatially, and temporal differences conceivably might also have complicated the results.

Relationships of the microsporidans seen in the various species of amphipods could not be decided on the basis of material fixed and prepared as it was. It would be interesting to determine whether the parasites of *Unciola* spp. and *Ampelisca vadorum* are the same or different species, and what their relationship is to the *A. agassizi* parasite. There were some differences in the habits and the developmental stages present in the three amphipods. Vegetative stages were common in the case of the *A. vadorum* parasite and fairly common in *Unciola* spp., but usually rare or absent in *A. agassizi*. Several different tissues were infected in *A. vadorum*, but excepting a few infections in nervous tissue, only abdominal muscle was infected in *Unciola* spp. and *A. agassizi*. Previous investigators have found that microsporidan infection is well tolerated by amphipod hosts, and that defense reactions against these parasites generally are limited and may come into play mainly when host tissue becomes necrotic (reviewed by Bulnheim 1975). The muscle-inhabiting microsporidan of *A. agassizi* is obviously a primary parasite of that species and is seldom attacked by the host. However, the similar parasite of *Unciola* spp. often either provokes attack merely by its presence or damages the muscle so that a response occurs to the necrotic tissue. In either event, it is possible that this parasite is not fully adapted to *Unciola* spp., because arthropods are known to be less tolerant of non-adapted parasites (Salt 1970; Unestam and Weiss 1970)

With exception of the muscle-infecting species from *A. agassizi*, microsporidans are not common parasites of benthic amphipods in the areas sampled, even considering that some infections must have been missed because not all would be seen in the limited number of sections examined from each amphipod.

Sampling methods used in the survey do not lend themselves to precise studies on progression of parasitic infections through particular populations. Sampling cannot be done often enough to show if and when additions to populations (with perhaps different prevalences of parasites) are provided by immigrating juveniles or other stages of these short-lived animals. Further, populations may not be

homogeneous over the area sampled at a single station. Sediment sampling with a grab is imprecise, as the different depths of samples taken at stations 47 and 48 on cruises E and F testify (Table 3). It is probable that return to an exact location was never accomplished. Even if populations were homogeneous, predation by fish, and other short-term disturbances, may cause local impoverishment of populations or differences in population composition that would not be detected in the necessarily blind sampling done with a Smith-McIntyre grab.

A general pattern does emerge. In the area surveyed, microsporidans are dominant parasites of the most numerous and ubiquitous species, *A. agassizi*, but are rare in all other species. This may be a reflection of the fact that only *A. agassizi* consistently occurred in dense populations at certain stations at all sampling times, a circumstance that would promote spread of a host-specific and horizontally transmitted parasite.

ACKNOWLEDGMENTS

Thanks are due to Frank Steimle and Robert Reid of the Northeast Fisheries Center Sandy Hook Laboratory, and Linda Dorigatti, Gretchen Roe, and Sharon MacLean of the Oxford Laboratory, who collected the amphipods. Ann Frame, Sandy Hook Laboratory, provided expert advice and training in identification of amphipods. Linda Dorigatti identified material from cruises A-C, and along with Gretchen Roe, Dorothy Howard, and Cecelia Smith of the Histology Section, Oxford Laboratory, prepared the specimens for histological examination. Ann Cali, Rutgers University, Newark, NJ, reviewed the manuscript and provided identification of the muscle-inhabiting microsporidan of *A. agassizi*.

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LONG-TERM RESPONSES OF THE DEMERSAL FISH ASSEMBLAGES OF GEORGES BANK

William J. Overholtz[1] and Albert V. Tyler[2]

ABSTRACT

The resilience of demersal fish assemblages on Georges Bank was investigated with data from seasonal bottom trawl surveys conducted by the Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Massachusetts, from 1963 to 1978. Cluster analysis proved to be a useful statistical method for delineating assemblage boundaries and associated species. Assemblages persisted over the long-term and changed spatial configuration only slightly on a seasonal basis. Declines in biomass, numerical density, and changes in relative abundance occurred ranging from mild to severe. Assemblage changes were probably triggered by intense fisheries as well as inherent trophic dynamics of component species. Results have useful multispecies management connotations. The assemblage concept appears to be an appropriate operational or conceptual framework for further management and modeling applications.

Most community ecological studies have necessarily concentrated on the short-term aspects or seasonality of assemblages. Typically 1 to 3 yr of field measurements are analyzed with information theory, niche breadth procedures, or multivariate statistical methods. Demersal fish assemblages in particular have been investigated in a number of locations [see studies by Tyler (1971), Oviat and Nixon (1973), Stephenson and Dredge (1976), Hoff and Ibara (1977), Gabriel and Tyler (1980), and Inglesias (1981)]. The recurrent theme in most of these studies centers around seasonally varying diversity because of environmentally induced migration, temperature usually acting as the dominant driving variable.

Unfortunately, many interesting questions cannot be addressed in these studies because of their short-term horizon. It is important to consider the long-term ramifications of fishery system responses. The temporal scale referred to here as "long-term" does not refer to geologic time, but rather ecological time, the span of years during which the actions of fishery ecologists evoke system responses. Fishery ecologists are limited in their ability to function within this time frame. For instance, a plant ecologist could predict with some certainty the type of forest that would eventually occupy a cleared site, if left undisturbed, but comparable knowledge for fishery systems is lacking, especially in the marine environment.

Are fish assemblages stable? How do they respond to exploitation? Holling (1973) investigated system responses to man's activities, showing that in closed systems, such as freshwater lakes, the propensity to remain stable is high, but not infallible. Smith (1972) critiqued the Great Lakes experience, concluding that the activities of man, notably fishing and pollution, when coupled with biological interactions, caused significant community alterations in this system. Few marine studies, with the exception of Soutar and Isaacs (1969), Sutherland (1980), DeVries and Pearcy (1982), and some general overview papers (Brown et al. 1976; Richards et al. 1978), have stressed the long-term temporal and spatial aspects of marine system response.

Longer term temporal and spatial questions were examined with data from research conducted at the Northeast Fisheries Center (NEFC) (Grosslein 1969). Concentrating on Georges Bank, we used cluster analysis to produce yearly fall and spring dendrograms for the period 1963-78 and 1968-78, respectively. Assemblages were defined, component species were identified, distributional maps plotted, and the information was examined to elucidate long-term temporal and spatial patterns. Further analyses led to trajectories of species catch-per-unit-effort (CPUE), assemblage total biomass, estimates of intra-assemblage diversity, and other measures of community response. It is suggested that fishing, coupled with interspecific interactions, appeared to have played a major role in determining trends in the Georges Bank assemblages.

[1]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331; present address: Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331; present address: Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada.

Manuscript accepted November 1984.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

METHODS

Georges Bank, a large, submerged, marine plateau, is located off the northeastern coast of the United States (Fig. 1). It has been the site of an intense fishery for several centuries, and a large international fleet exploited the area from the 1960's to the mid-1970's. The NEFC has conducted annual bottom trawl surveys on the Northwest Atlantic continental shelf since the autumn of 1963. Annual spring surveys commenced in 1968 and, in addition, several summer and winter cruises have been undertaken on an intermittent basis. Surveys were conducted from Nova Scotia to Hudson Canyon from 1963 to 1966 and coverage was extended to Cape Hatteras beginning in 1967. Grosslein (1969) and Azarovitz (1982) described the details and justification for the surveys, but a brief summary is appropriate.

The objective of the surveys is to obtain statistically meaningful abundance estimates of the offshore marine fish populations in the aforementioned areas. Secondary objectives included the collection of data for distribution studies, age and growth determinations, predator-prey interactions, and a host of special purpose investigations. The potential area was divided into zones (strata) based on depth and biological considerations. Stratified random samples were selected with allocation to each strata proportional to its area. A 30-min sample with a standardized research bottom trawl and a 1.25 cm cod end liner was accomplished. All fish, as well as major invertebrates, were sorted to species, weighed, and measured, and some fish were sampled for other

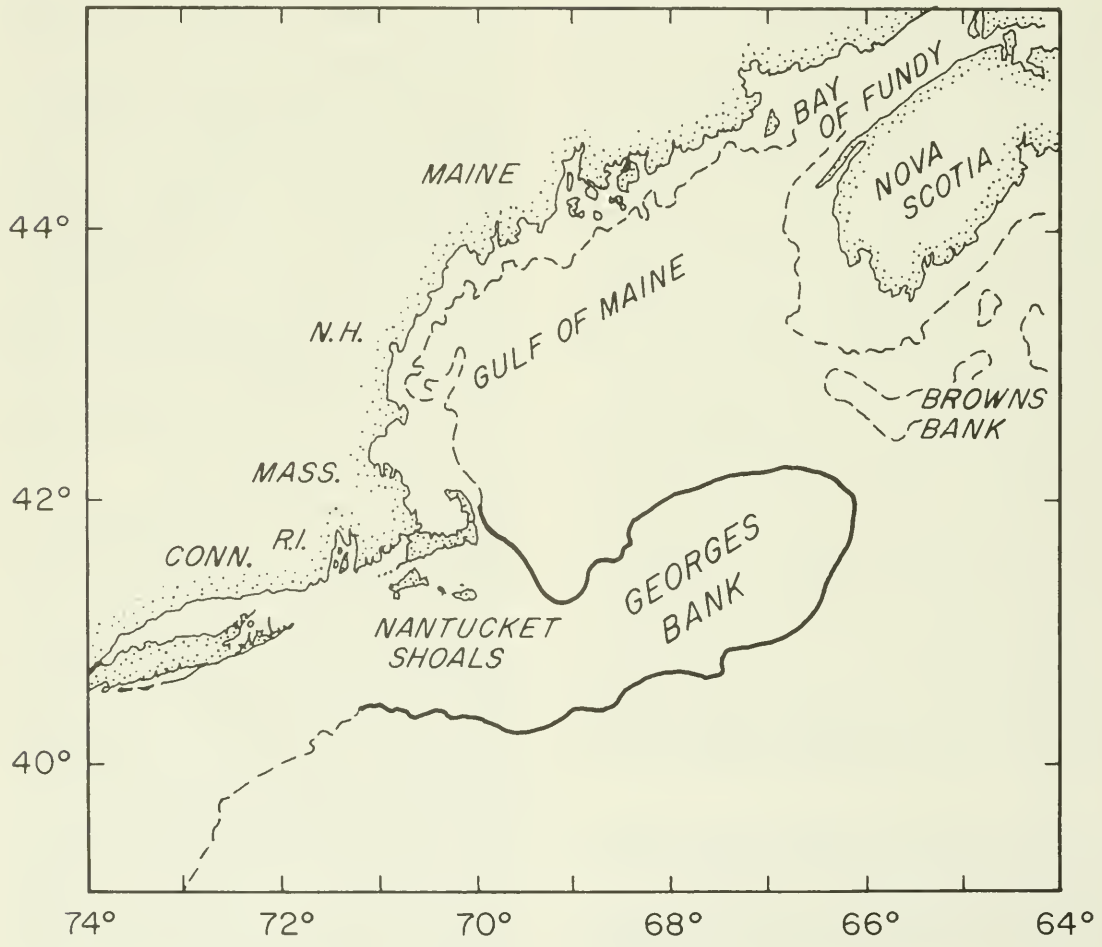

FIGURE 1.—Georges Bank and Gulf of Maine region with shoreline place names and other associated geographical landmarks.

analyses. Sampling frequency averages about one station for every 250 mi^2 or roughly 300 locations in a normal survey from Cape Hatteras to Nova Scotia.

Data from a selected portion of this time series was used in cluster analyses that defined demersal fish assemblages. Specifically, a group of 36 species representing the dominant fishes on Georges Bank, were chosen as the focus for the investigation (Table 1). This choice was based on a preliminary examination of the data to determine which species were most important in terms of biomass and numerical density. Catches (kg) for each of the species from every station in a particular cruise were organized into a data matrix and processed with an agglomerative cluster analysis program (Keniston 1978). To remove skewness in the species matrices, we transformed the data prior to clustering by using an ln $(x + 1)$ conversion. Station dissimilarities were calculated by using the Bray-Curtis dissimilarity index, an ecological distance measure that is sensitive to dominant species (Clifford and Stephenson 1975; Boesch and Swartz 1977).

TABLE 1.—Species cited by common name in the text.

Common name	Scientific name
Spiny dogfish	*Squalus acanthias*
Winter skate	*Raja ocellata*
Little skate	*Raja erinacea*
Smooth skate	*Raja senta*
Thorny skate	*Raja radiata*
Atlantic herring	*Clupea harengus*
Alewife	*Alosa pseudoharengus*
Offshore hake	*Merluccius albidus*
Silver hake	*Merluccius bilinearis*
Atlantic cod	*Gadus morhua*
Haddock	*Melanogrammus aeglefinus*
Pollock	*Pollachius virens*
White hake	*Urophycis tenuis*
Red hake	*Urophycis chuss*
Cusk	*Brosme brosme*
American plaice	*Hippoglossoides platessoides*
Summer flounder	*Paralichthys dentatus*
Fourspot flounder	*Paralichthys oblongus*
Yellowtail flounder	*Limanda ferruginea*
Winter flounder	*Pseudopleuronectes americanus*
Witch flounder	*Glyptocephalus cynoglossus*
Windowpane	*Scophthalmus aquosus*
Gulf stream flounder	*Citharichthys arctifrons*
Atlantic mackerel	*Scomber scombrus*
Butterfish	*Peprilus triacanthus*
Bluefish	*Pomatomus saltatrix*
Blackbelly rosefish	*Helicolenus dactylopterus*
Longhorn sculpin	*Myoxocephalus octodecemspinosus*
Sea raven	*Hemitripterus americanus*
Cunner	*Tautogolabris adspersus*
American sand lance	*Ammodytes americanus*
Atlantic wolffish	*Anarhichas luptus*
Ocean pout	*Macrozoarces americanus*
American goosefish	*Lophius americanus*
Short-finned squid	*Illex illecebrosus*
Long-finned squid	*Loligo pealei*

The resulting dissimilarity matrix was used in a group average fusion strategy to combine stations with similar species distributions (Clifford and Stephenson 1975). These station combinations were displayed in dendrograms, which were examined and assemblage groups were chosen by two criteria: large-scale separations, as shown in Figure 2, and dissimilarity levels. Stations from these assemblage groups were plotted on cruise maps from the original sampling plan and areas were delineated. This process was repeated for all spring and fall cruises to provide a consecutive series of maps, which were then examined for continuity (Fig. 3). Finally, data from several consecutive years were pooled to delineate assemblages designated, based on nearby geographic features or depth zones.

Species lists were prepared for the assemblages outlined in the pooled cluster results, and data were analyzed to further define the structure of each group. Length frequencies from species in the different assemblages were used to separate life history stages and catch-per-tow data were used to investigate trends in distribution and abundance. Examination of food habit data in the literature and NEFC documents gave further insight into assemblage structure. Trajectories of assemblage CPUE for selected species were plotted and examined for long-term trends. Total assemblage CPUE was also investigated and compared with previous trends reported by other authors for the region.

Gradient analyses were performed with the objective of explaining species distributions based on a set of location, physical, and chemical variables. Canonical correlations, using information on latitude, longitude, depth, bottom temperature, bottom oxygen, and bottom salinity, were employed to define possible gradients that might be useful indicators of species distribution (Pimentel 1979). Data for the autumn cruise were obtained from measurements of bottom temperature and depth made aboard the RV *Albatross IV* (U.S.A.) 20 October to 5 November 1976, and corresponding information on bottom salinity and oxygen from the RV *Anton Dohrn* (Federal Republic of Germany) 14 November to 1 December 1976. Information for the spring cruise was procured from measurements of bottom temperature and depth from the RV *Albatross IV*, 17 April to 3 May 1978, and salinity and oxygen data that was obtained from the RV *Argus* (Union of Soviet Socialist Republics) from 13 to 28 April 1978; these two data sets were chosen because they corresponded closely in time to the available station information.

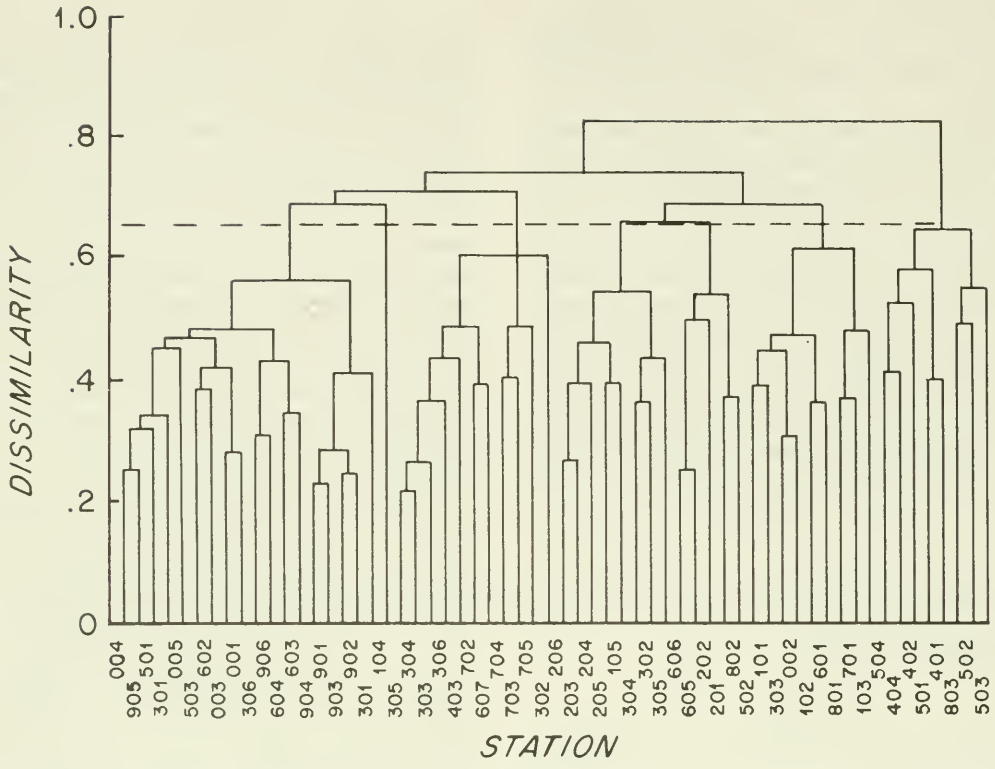

FIGURE 2.—Typical dendrogram, autumn 1966, showing cluster station groups and dissimilarities. Dashed line indicates a dissimilarity of 0.65.

RESULTS

Five important assemblage groups were present on Georges Bank from fall 1963 to 1978. For reference, we name these groups: Slope and Canyon, Intermediate, Shallow, Gulf of Maine Deep, and Northeast Peak. A consistent spatial pattern emerged as consecutive fall cruises were examined and plotted. The same five groups appear to have been present in similar locations since 1963. These five assemblages were present at the mid- and endpoints of the fall time series also (Fig. 3). The groups appear to change their spatial configuration slightly on an annual basis, but the general area of each group was maintained. Lists of the dominant species in each assemblage are given in Table 2.

The total area that each assemblage encompassed through time (years) was delineated by pooling the observations from consecutive years. Figure 4 shows an example of a representative assemblage from the spring and fall, respectively. The groups overlapped surprisingly little through time with the exception of a few border stations along adjacent assemblages.

TABLE 2.—Assemblage species associations from cluster results (demersal species only).

Slope and canyon:	Red hake
Silver hake	Summer flounder
White hake	Yellowtail flounder
Red hake	Winter flounder
Gulf stream flounder	Windowpane
Offshore hake	Longhorn sculpin
Fourspot flounder	Sea raven
Blackbelly rosefish	Ocean pout
American goosefish	Sand lance
Intermediate:	American goosefish
Winter skate	Gulf of Maine Deep:
Little skate	Thorny skates
Red hake	American plaice
Silver hake	Witch flounder
Atlantic cod	White hake
Haddock	Silver hake
Sea raven	Atlantic cod
American goosefish	Haddock
Ocean pout	Cusk
Longhorn sculpin	Atlantic wolffish
Yellowtail flounder	Northeast Peak:
Shallow:	Thorny skate
Winter skate	Atlantic cod
Little skate	Haddock
Silver hake	Pollock
Atlantic cod	White hake
Haddock	Winter flounder
Pollock	Ocean pout
White hake	Longhorn sculpin

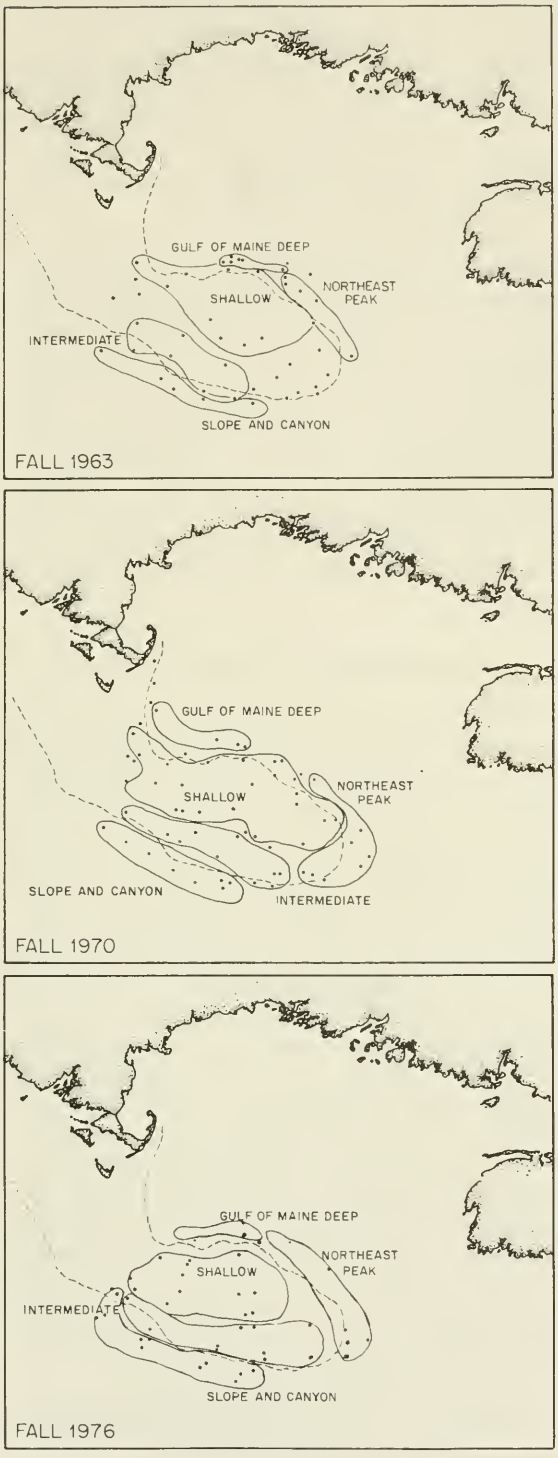

FIGURE 3.—Georges Bank assemblages for three autumn surveys 1963, 1970, 1976.

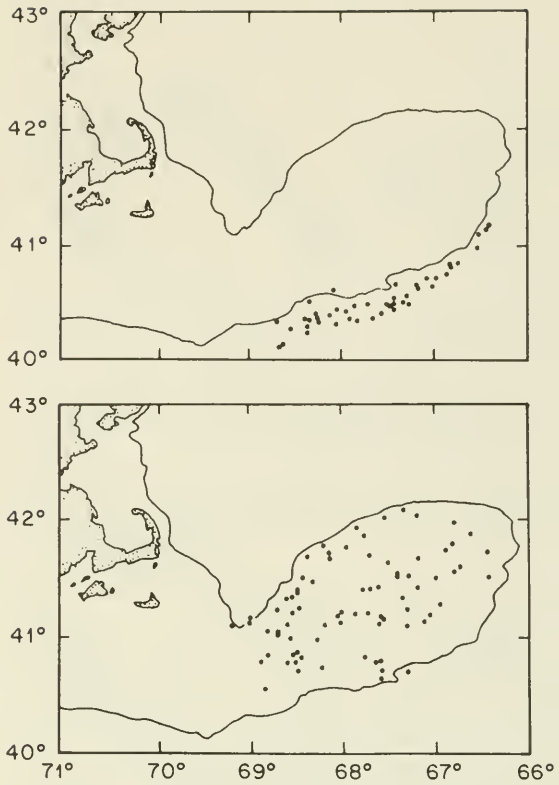

FIGURE 4.—Sample pooled station distributions for the Slope and Canyon assemblage, spring 1968-73 (top panel) and the Shallow assemblage, autumn 1963-67.

Data for all cruises were pooled by season and used to generate composite maps of general assemblage areas, for the spring and autumn (Fig. 5). The Slope and Canyon assemblage appears to encompass a similar area regardless of season, while some of the other assemblages changed slightly. The Shallow assemblage covered most of Georges Bank in the spring (Fig. 5) and was slightly smaller in the fall (Fig. 5). The Intermediate assemblage is somewhat larger in the fall (Fig. 5), suggesting a migration of the species in this area to shallower water as the year progresses. Assemblages in the spring appear to follow depth contours resulting in the elongate shape of the groups at this time (Fig. 5). The Northeast Peak Interior (NPI) and Northeast Peak-Gulf of Maine Deep (NPGM Deep) assemblages show definite seasonal spatial changes when compared with the Gulf of Maine Deep (GM Deep) and Northeast Peak assemblages in the fall (Fig. 5). The general shape and location of the fall assemblages suggests that a different set of oceanographic and biological forcing factors are important in deter-

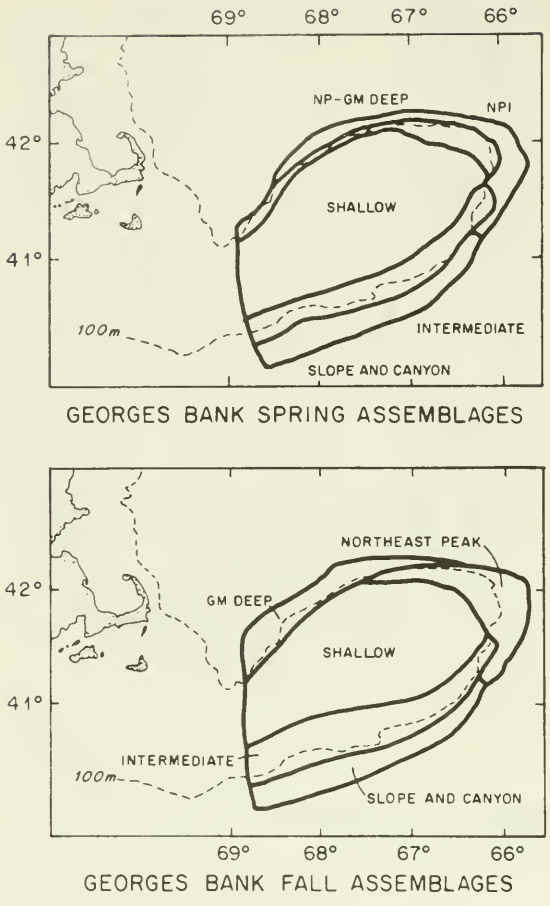

FIGURE 5.—Composite maps showing seasonal changes in the Georges Bank assemblages and their approximate areas. NPI = Northeast Peak Interior; NPGM Deep = Northeast Peak-Gulf of Maine Deep; GM Deep = Gulf of Maine Deep.

mining the distribution of fish. The Northeast Peak assemblage, for instance, spans several depth zones and encroaches on the Shallow assemblage, reducing its area during this part of the year.

The assemblage maps presented in Figure 5 were useful for organizing the 36 species of Table 1 into their corresponding demersal subunits (Table 2). Four basic species categories were defined in the various assemblages. These included ubiquitous species, resident species, periodics, and those resident species present in several assemblages during different parts of their life history. Ubiquitous species, such as ocean pout, goosefish, sea raven, and Atlantic cod, were found with regularity in almost all of the assemblages. Resident species, such as little skate, winter skate, longhorn sculpin, yellowtail flounder, winter flounder, American plaice, and witch flounder, were present in only one or two assemblages in abundance. Periodic or seasonal migrants include bluefish, butterfish, and mackerel, as well as short-finned squid and long-finned squid. These species moved in and out of the various assemblages on a seasonal basis with temperature being a likely dominant force, and were often highly variable in terms of their abundance and were therefore not included in Table 2.

A number of species, including silver hake, red hake, white hake, and haddock, were present in more than one assemblage as different life history stages. Silver hake, for example, are found in the Slope and Canyon and Shallow assemblages, with adults on the average, occurring more frequently in the Slope and Canyon and Gulf of Maine Deep assemblage, while juveniles are more abundant in the Shallow assemblage. It appears that for many of the abundant fish species on Georges Bank, adults occupy the deeper peripheral assemblages while juveniles of these same species occupy the shallower zones during much of the year.

ASSEMBLAGE TRAJECTORIES

Assemblage CPUE indices were calculated for several of the spring and fall assemblages and used for evaluating temporal trends in total catch and catch by species. Assemblage CPUE declined dramatically in the mid-1960's to early 1970's in four of five Georges Bank assemblages in fall (Fig. 6). In particular, research catches in the Shallow, Northeast Peak, and Gulf of Maine Deep assemblages reached all-time lows in the early 1970's, coincident with large increases in international effort and landings at that time (Figs. 6, 7). International effort, measured in thousands of days fished, increased threefold over the period 1960-69 (Fig. 7). Assemblage biomass showed some signs of recovery in the late 1970's when good year classes of Atlantic cod, haddock, and other species occurred and international effort declined due to the Magnuson Fishery Conservation and Management Act of 1976 (Figs. 6, 7).

Research catch of silver hake, fourspot flounder, red hake, white hake, and black belly rosefish remained nearly stable over the spring period (1968-75), then increased abruptly after 1976 due to increases in the silver hake (Fig. 8A).

Total catch for the fall time series was also stable for most years, until 1972 when silver hake and red hake abundance fluctuated (Fig. 8B).

Figure 8C shows the trends in percent by weight for the five species during fall indicating a change in biomass dominance for silver hake and red hake. Blackbelly rosefish and fourspot flounder showed the

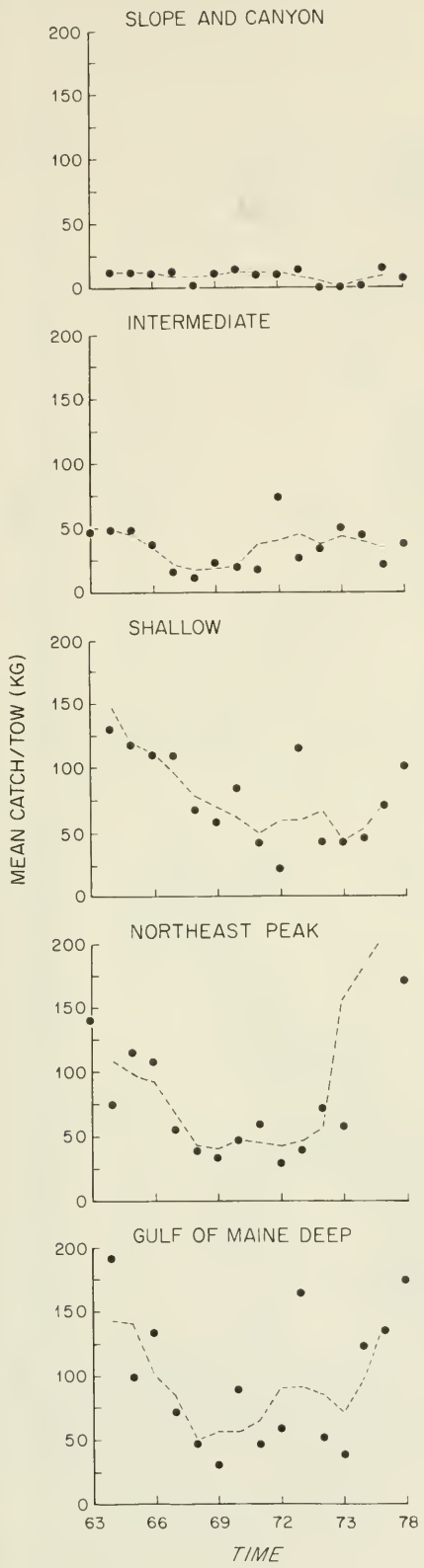

Figure 6.—Mean catch per tow (kg) from NEFC Georges Bank bottom trawl surveys for autumn 1963-78 for the five assemblages. Dashed line indicates a 3-yr moving mean of the plotted data points.

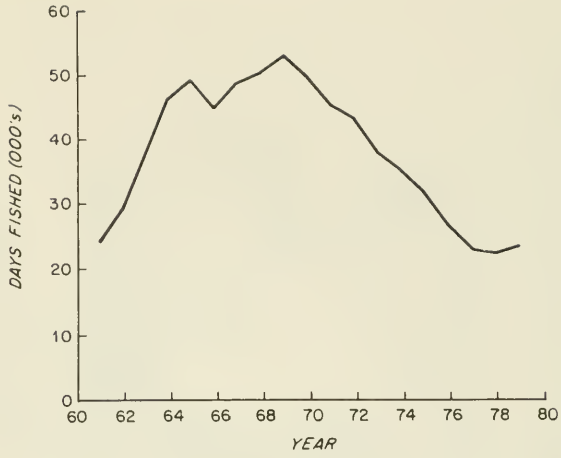

Figure 7.—Unstandardized effort data in thousands of days fished for the Georges Bank demersal fishery, all countries, for 1961-79, expressed as 3-yr moving means.

same trends as in the former case, but represented more of the catch on a percent weight basis in the later years of the fall time series (Fig. 8C). Gulf Stream flounder was actually one of the more important species numerically during the mid-years of the series (Fig. 8D). The same general trend for red and silver hake, and the other species is apparent in the percent by numbers data (Fig. 8D).

The shallow assemblage was much more diverse than the Slope and Canyon assemblage. The major species of importance were Atlantic cod, winter skate, longhorn sculpin, little skate, yellowtail flounder, and haddock. Mean catch per tow in the fall time series declined dramatically from 202 kg in 1963 to 22 kg in 1972 and subsequently rose to 99 kg in 1978 or about one-half the 1963 value (Fig. 6). Winter flounder, longhorn sculpin, and winter skate appear to have remained fairly constant in abundance over the spring time period, while Atlantic cod, windowpane flounder, and little skate displayed an increasing trend in biomass (Fig. 9A). Yellowtail flounder and haddock showed declining mean catches over this interval. The fall time series, since it is longer, clarifies some of the observed spring trends. Cod and winter flounder CPUE remained relatively stable over the fall period, while windowpane flounder, winter skate, and little skate appear to have increased from 1972 onward (Fig.

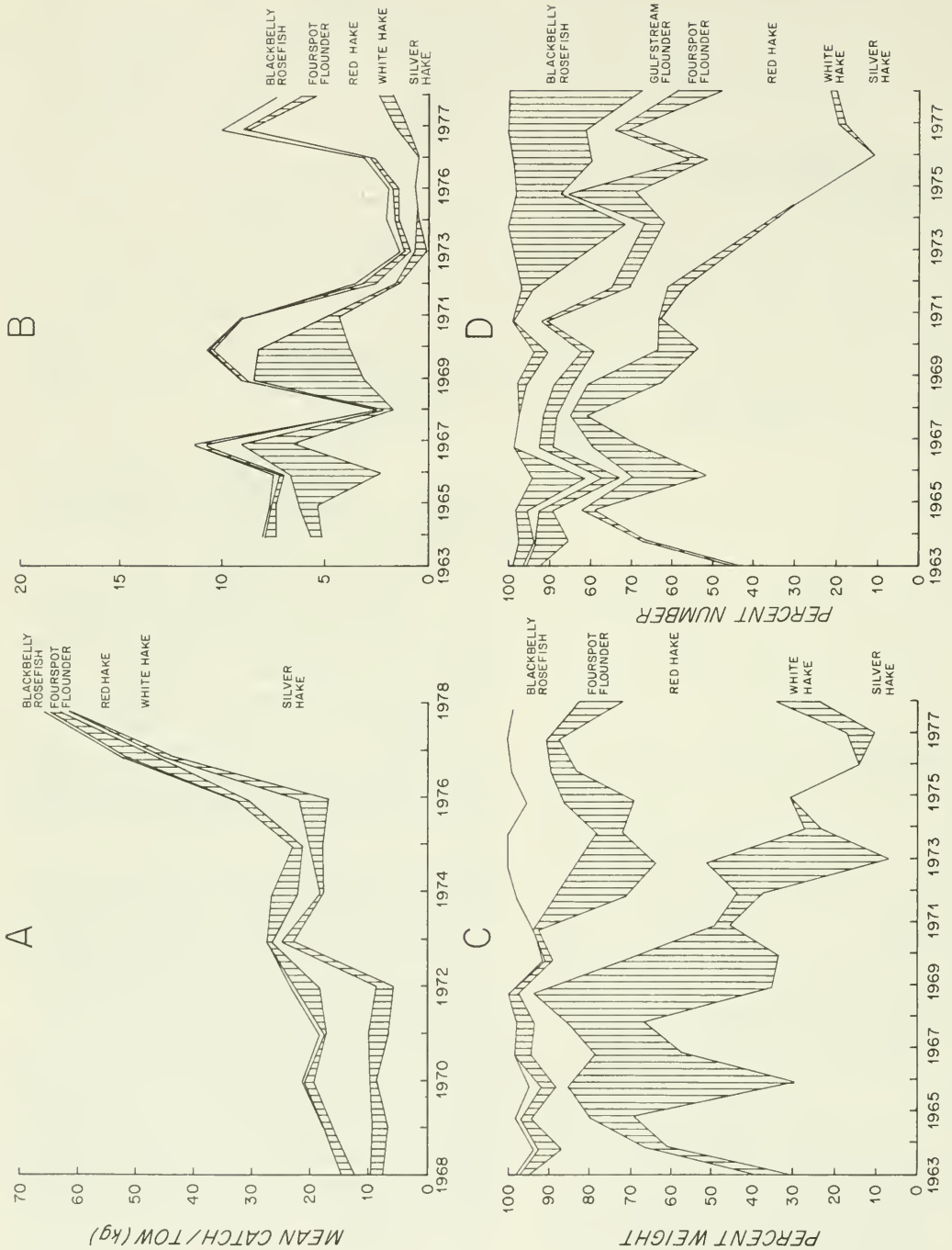

FIGURE 8.—Responses of species from the Slope and Canyon assemblage demersal fish community over the period 1963-78. Panels A and B express cumulative absolute abundance, mean catch/tow (kg) for spring 1968-78 and autumn 1963-78, respectively. Panels C and D show cumulative percent by weight and number, respectively, for autumn 1963-78.

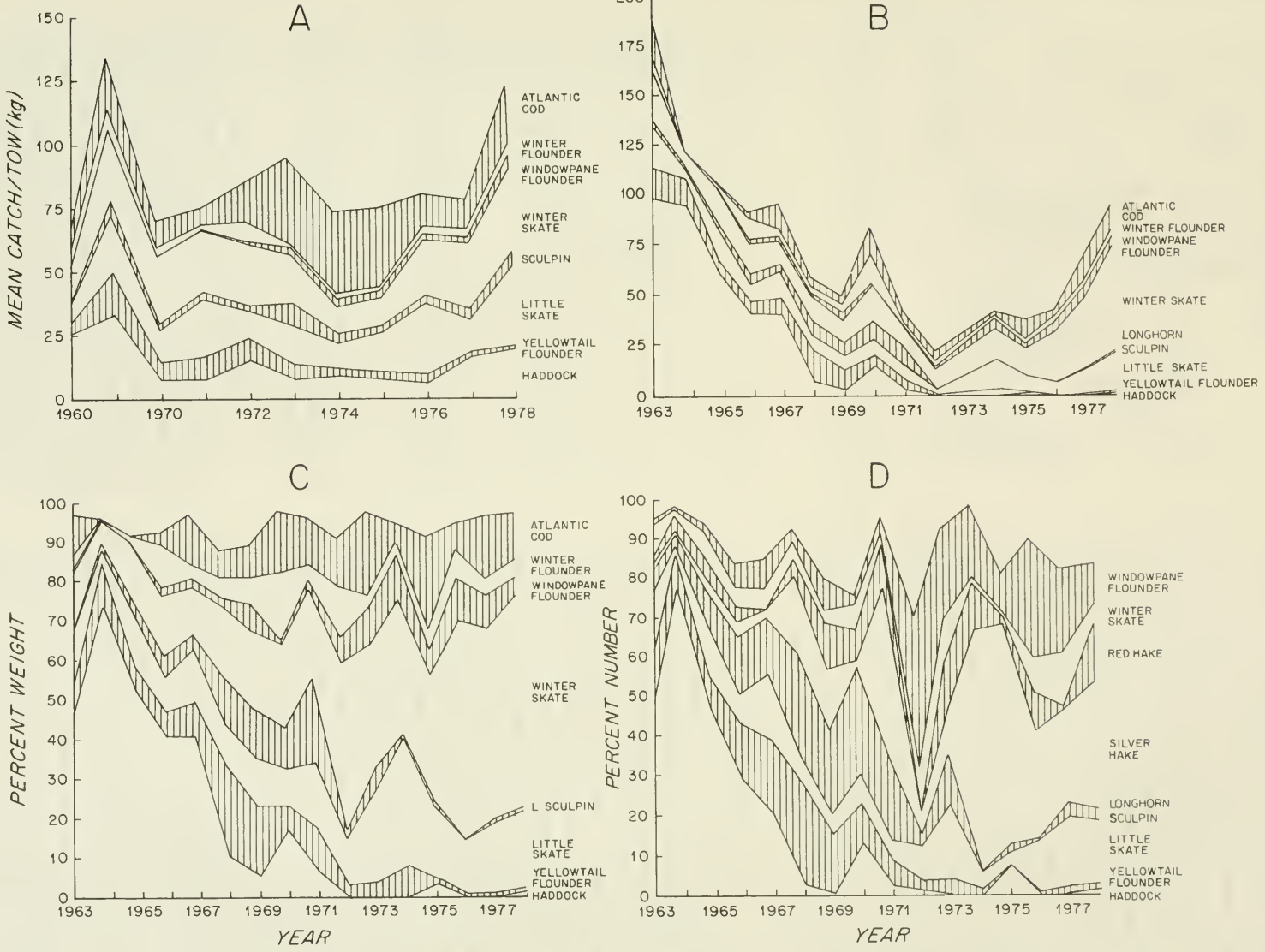

FIGURE 9.—Responses of species from the Shallow assemblage demersal fish community over the period 1963-78. Panels A and B express cumulative absolute abundance, mean catch/tow (kg) for spring 1968-78 and autumn 1963-78, respectively. Panels C and D show cumulative percent by weight and number, respectively, for autumn 1963-78.

9B). Haddock CPUE, on the other hand, declined dramatically from 97.3 kg in 1963 to 0 in 1972, remaining at very low levels of abundance in the later years. Yellowtail flounder fluctuated from 15 kg in 1963 to a low of 6 kg in 1966, increased from 1966 to 1969, and declined through 1978 (Fig. 8B).

An examination of trends in cumulative percent by weight and number trajectories for the Shallow assemblage highlighted some interesting points. Atlantic cod comprised a fairly constant proportion of the species biomass for all the years except 1964 and 1965. Longhorn sculpin, yellowtail flounder, and to a lesser extent winter flounder, made up an increasing part of the biomass of this assemblage during 1966-71 and then all declined in importance (Fig. 9C). Haddock, as previously noted, experienced a pronounced decline in abundance from the early 1960's and was only present at very low levels from 1972 to 1978. Winter skates, little skate, and windowpane flounder accounted for an increasing percent of the biomass in this assemblage from the early 1970's onward (Fig. 9C).

When cumulative percent by number was investigated, silver hake and red hake became important (Fig. 9D). Silver hake was the numerical dominant through most of the mid- and late 1970's. This trend was due entirely to increased numbers of juvenile silver hake that represented a small amount of biomass. This same phenomenon applies to red hake, which enjoyed several periods of increased abundance as a proportion of the total numerical density from 1963 to 1978. Winter skate numbers remained relatively unchanging from 1963 to 1976 and then rose slightly in the late 1970's. Trends for windowpane flounder, longhorn sculpin, little skate, yellowtail flounder, and haddock follow the cumulative absolute and percent weight data (Fig. 9B, C, D).

The other Georges Bank assemblages were investigated using the same techniques, but on a much less intense scale. Total mean catch/tow for the Intermediate, Gulf of Maine Deep, and Northeast Peak assemblages is displayed in Figure 6 for the fall surveys 1963-78. The trends in total CPUE follow the same basic patterns for all three groups, a high initial period followed by a decline and subsequent recovery in the mid- to late 1970's.

General decreases in the catch of thorny skates, haddock, and cod were responsible for the downward trend in CPUE for the Northeast Peak assemblage, but the recovery that occurred in the late 1970's was due primarily to increased haddock biomass (Figs. 6, 10). The Northeast Peak assemblage is fairly simple in species composition, and although some fluctuations in cumulative percent by weight occurred,

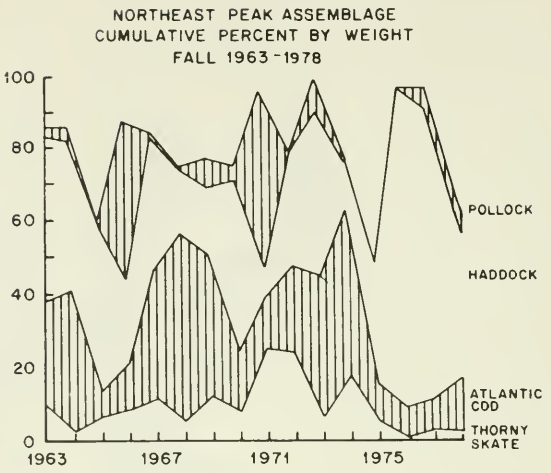

FIGURE 10.—Reponses of species from the Northeast Peak assemblage demersal fish community expressed as cumulative percent by weight for autumn 1963-78.

the same four species remained dominant over the period (Fig. 10.)

Time sequence cluster analyses were useful as further indicators of temporal trends in these groups. Species biomass for the Slope and Canyon assemblage did not appear to follow any clear long-term trend (Fig. 11). Enough fluctuation in CPUE occurred to mask any trend, and no clear pattern was established. This same analysis on the Shallow assemblage showed three distinct temporal clusters, composed of consecutive years (Fig. 11). Using this perspective and Figure 9, there appears to have been three periods of significant change in relative abundance during the fall time series; an initial period dominated by haddock, intermediate period with high yellowtail, longhorn sculpin, and winter flounder catches, and finally a group with little skate, winter skate, and windowpane flounder as the dominant species.

GRADIENT ANALYSIS

Gradient analyses of two selected Georges Bank data sets did not prove to be as useful as was hoped, but some information and insight were gained and the dimensionality of the large multivariate data sets involved was much reduced. The data set used in the fall 1976 canonical correlation analysis accounted for about 26% of the variation in species distribution for 32 selected species of interest. The variables included in the analysis were latitude, longitude, depth, bottom temperature, bottom salinity, and bottom oxy-

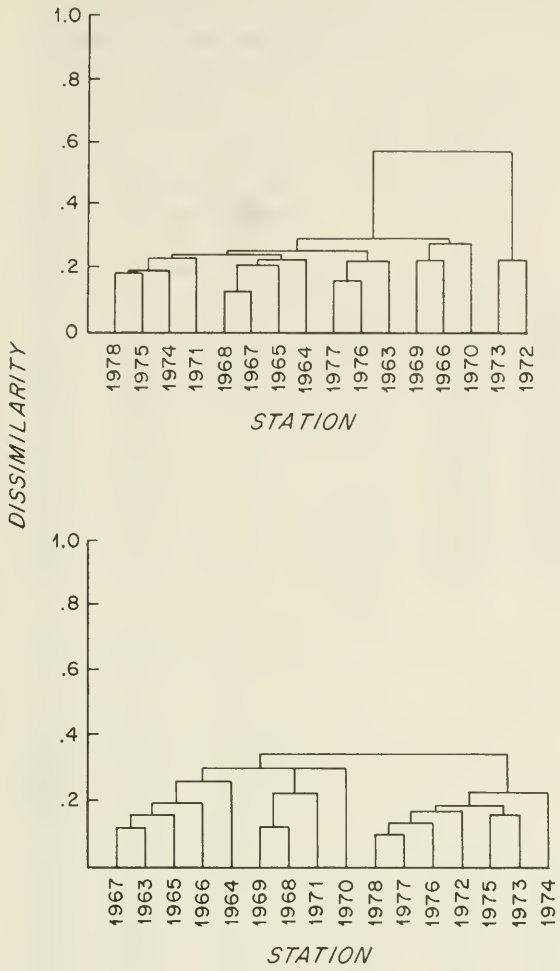

FIGURE 11.—Time sequence cluster analyses for autumn 1963-78 for the Slope and Canyon (top panel) and Shallow (bottom panel) assemblages on Georges Bank.

gen. The first three canonical axes accounted for 73.9% of this total, a cumulative redundancy of 19.0% (Table 3). The first canonical variable (CV) reflects the importance of depth and to a lesser degree bottom salinity, in determining the distribution of these species. Although none of the correlation loadings for CV1 are particularly high, the gadoids, as a group, show a positive trend. Many of the shallow-water species, such as little skate, winter skate, and most of the flounders, showed negative correlations with this canonical variable. The other two CV's reflect the location variables of latitude and longitude as well as bottom oxygen and salinity.

Since the gadoids and flounders appeared to show a group response to these distribution variables, we decided to use them in another analysis, excluding the other species (Table 3, Fall 1976 II). This data set explained 28.3% of the total variation in distribution for a selected set of 14 species (Table 3). The first canonical variable had a high correlation with latitude (r = 0.904) and the gadoids, as a group, were highly positively correlated with this CV (Table 3). It appears that although Georges Bank spans only about two degrees in total north-south latitudinal variation, this variable is useful for defining centers of gadoid biomass.

The third analysis did not reveal any new trends, accounting for 32.6% of the variation in species distribution. In general, then, although significant orthogonal canonical axes were defined in each of three data sets, the amount of variation that was actually explained was relatively small. There appear to have been trends in the distribution of some gadoid and flounder species, but the strength of these relationships was hardly firm. Most of the variation in species distribution was related to latitudinal, salinity, and depth differences.

DISCUSSION

Questions of community resilience (Pimm 1984) are meaningful because resource managers are faced with the dilemma of making decisions that may alter future community structure. Fishery managers, in particular, are unable to deal with the long-term consequences of their management decisions because they lack specific knowledge of ecosystem reponses. This idea may apply particularly to areas such as Georges Bank, where landings of each species are part of a multispecies otter trawl fishery. In this case the application of single species management to assemblages of fishes may result in simplification of the community such that less productive fish populations or those more vulnerable to fishing are reduced dramatically (Tyler et al. 1982). If this occurs, important trophic linkages may be precluded, economic viability may suffer, and management options may be removed indefinitely. At the present time the argument of these central issues is proceeding slowly in the literature and few, if any, management agencies are considering these types of questions in their decisions. We need, therefore, to begin to investigate the long-term temporal scale of communities so that ecologists and managers can begin to function in terms of ecological time instead of just a framework for short-term reaction.

Declines in total finfish abundance on the continental shelf of the northeastern United States reached unprecedented levels over the period 1965-74 (Brown et al. 1976). Not only had biomass declined,

TABLE 3.—Canonical variable (CV) loadings for fall 1976 and spring 1978 gradient analyses, with canonical correlation coefficients (Rc), amount of variation explained by each canonical axis (% variation), and total variation in species distribution explained by the environmental data.

	Fall 1976 I			Fall 1976 II			Spring 1978 I		
	CV1	CV2	CV3	CV1	CV2	CV3	CV1	CV2	CV3
Spiny dogfish	−0.509	0.149	0.232				−0.089	0.105	0.111
Winter skate	−0.263	0.342	−0.244				−0.176	−0.377	0.058
Little skate	−0.428	0.113	−0.163				−0.015	−0.437	0.142
Smooth skate	0.552	−0.117	−0.144				0.333	0.210	−0.204
Thorny skate	0.387	0.017	0.063				0.534	0.416	0.188
Sea herring	0.003	0.081	0.058				0.084	−0.147	0.068
Alewife	−0.023	0.097	0.161				0.433	0.086	0.104
Offshore hake	0.456	−0.408	−0.100	−0.147	0.613	0.284			
Silver hake	0.285	0.203	0.536	0.607	0.332	0.027	−0.237	0.637	−0.328
Atlantic cod	0.059	0.544	0.195	0.600	−0.263	0.048	0.262	−0.534	0.177
Haddock	0.370	0.525	0.131	0.647	−0.069	−0.235	0.383	−0.300	0.072
Pollock	0.337	0.158	0.199	0.439	0.274	0.167	0.425	0.209	0.015
White hake	0.564	−0.022	0.341	0.447	0.614	0.083	−0.030	0.527	0.055
Red hake	−0.109	−0.109	0.034	−0.220	−0.043	−0.460	0.303	0.616	0.057
American dab	0.281	0.048	0.362	0.395	0.365	0.141	0.409	−0.035	−0.026
Summer flounder	−0.245	−0.124	−0.102	−0.246	−0.111	0.126	−0.427	0.309	0.303
Fourspot flounder	−0.235	−0.265	0.210	−0.326	0.051	−0.588	−0.417	0.418	0.366
Yellowtail flounder	−0.158	0.324	−0.083	0.115	−0.419	−0.095	0.080	−0.442	0.144
Winter flounder	−0.145	0.364	0.078	0.295	−0.324	0.114	0.109	−0.301	0.040
Witch flounder	0.179	−0.267	0.140	−0.107	0.407	−0.187	0.368	0.138	−0.225
Windowpane	−0.326	0.165	−0.351	−0.087	−0.439	0.504	−0.527	0.041	0.251
Butterfish	−0.279	−0.415	0.405						
Blackbelly rosefish	0.359	−0.544	0.050				−0.295	0.529	−0.199
Longhorn sculpin	−0.078	0.432	−0.136				0.101	0.478	0.068
Sea raven	−0.034	0.432	−0.092				−0.500	0.034	0.194
Cunner	−0.082	0.198	0.023						
American sand lance	−0.134	0.043	−0.079				0.130	−0.125	0.224
Atlantic wolffish	0.011	0.240	0.106				0.233	0.073	0.358
Ocean pout	−0.043	0.265	0.122				−0.133	−0.316	0.034
American goosefish	0.145	−0.073	0.184				−0.261	0.414	−0.039
Short-finned squid	0.249	0.284	0.303				−0.275	0.169	0.072
Long-finned squid	−0.471	−0.239	−0.379				−0.256	0.399	−0.077
Variables									
Latitude	0.306	0.922	0.074	0.904	−0.333	0.066	0.878	0.012	−0.131
Longitude	−0.458	−0.164	0.597	−0.004	0.064	0.118	0.240	−0.032	0.474
Depth	0.885	−0.432	0.049	0.030	0.849	−0.071	−0.107	0.792	−0.448
Bottom temp.	−0.179	−0.696	−0.233	−0.590	0.258	0.366	−0.252	0.720	−0.465
Bottom salinity	0.463	−0.547	0.422	−0.107	0.753	−0.586	−0.374	0.909	−0.133
Bottom oxygen	−0.316	0.450	−0.581	0.041	−0.613	0.407	0.199	−0.908	0.144
RC	0.975	0.961	0.874	0.871	0.841	0.750	0.979	0.968	0.943
% variation	8.2	7.2	3.6	11.1	9.1	4.3	9.2	11.8	2.8
Significance	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Total variation		25.7			28.3			32.6	

but total effort on Georges Bank increased several times (Fig. 7). The assemblage trends examined in this paper can be linked to these high levels of effort.

During this time period, seasonal bottom trawl surveys monitored trends in finfish abundance over the area from the Gulf of Maine to Cape Hatteras. This survey proved invaluable to fish stock assessment work because changes in the relative abundance of most of the commercial species were followed closely and were highly correlated with commercial catch, effort, and other indices (Clark 1979). Other species of ecological, perhaps not commercial importance, were also routinely and closely monitored over this time. The spring and fall bottom trawl survey provided an excellent means for assessing community or assemblage responses over this time period.

Cluster analysis, with the Bray-Curtis dissimilarity index and group average fusion method, proved helpful for defining demersal fish assemblages on Georges Bank. Recent studies confirm the value and applicability of the Bray-Curtis index (Bloom 1981). This method provided a means for collapsing the multidimensional nature of the spring and fall Georges Bank survey cruises into smaller, more easily interpreted, units. It was then possible to investigate not only long-term temporal and spatial persistence questions, but also intraspecific responses within the particular assemblage of interest.

Not only did seasonal Georges Bank assemblages maintain their temporal integrity over the periods 1963-78 in the fall and 1968-78 in the spring, but they also appear to have retained their spatial configuration for the most part as well. The results of this study indicate that although changes in species composition and relative abundance occurred in varying degrees in all the assemblages, they remained continuous in time and space.

Although many of the species on Georges Bank are found in several assemblages, it appears that each of the five groups has enough large-scale variation in biomass, species composition, and relative abundance to make each of the assemblages unique. Also at least one or two dominant Georges Bank species occupy each assemblage, for example, the bulk of the haddock stock occurs in the Northeast Peak group. Thus, even though some assemblages changed dramatically in terms of species richness and relative abundance, the spatial integrity of each complex was preserved over time.

The energy budget of Georges Bank can serve as a plausible explanation for the particular species distributions we found. Georges Bank is a dynamic ecosystem driven by a complex and unique nutrient advection system. Its shallow topography and geographic location, with constant mixing of the water column and lack of stratification, does not lead to the usual nutrient limitation of primary productivity (Sutcliffe et al. 1976; Cohen et al. 1982). Instead of the usual spring and fall pulse in primary production, the region is characterized by high productivity from April to November. Yearly primary production levels are as high as 450 gC/m^2 per yr in the shallow (< 100 m) zone of Georges Bank (Cohen et al. 1982). This shallow mixed zone encompasses the same area as the Shallow and Intermediate assemblages delineated in our cluster analysis results. The area is dominated by fish that feed on invertebrates. Primary prey items for these species include euphausiids, copepods, mysids, amphipods, and other benthic invertebrates. This part of the ecosystem is fairly closely tied to primary production, and its component species may compete for food resources during their early life history (Pitt 1970; Bowman 1981; Overholtz 1982). Predation, too, may be an important biological mechanism for determing trends in this assemblage (Overholtz 1982). The other assemblages that we have described in this analysis occur along the fringes of Georges Bank at the shelf-slope interface. These shelf break groups contain the major adult demersal fish stocks found in the area with the exception of yellowtail flounder. These peripheral assemblages are dominated by large predators that are generally piscivorous, with little, if any, dietary overlap (Langton and Bowman 1981).

The gradient analyses suggest that about 25% of the total variation in species biomass distribution can be explained with the variables used in the study. This result was surprising at first, since we felt that the variables we used would explain much more of the variation than this. However, considering the fact that other important biological factors, such as predation, fishing, competition, and food preferences were not included in the analysis, it is probably a realistic percentage. Perhaps an analysis that included the whole east coast would account for much more variation because a wider range of conditions would exist.

Other studies that have successfully explained species distributions usually occur in habitats with very strong physical or chemical gradients, such as mountain forests or estuaries (Whitaker 1967; McIntire 1973). Either the actual gradients were not strong enough to explain more than a small percentage of the species distribution or those other factors were more important.

The questions of resilience and stability of demersal fish assemblages that were defined and investigated in this study have implications for the management of Georges Bank. This study provides a useful conceptual framework for managing many of the demersal fish stocks in this area. Not only were stable zones with specific resident fishes delineated, but they were present over the long-term record. Species components of fall assemblages are indicators of general distributions that represent the location of major fish stocks during the productive portion of the year. Long-term responses observed in the Georges Bank community indicate the propensity for adjustment or resilience (Holling 1973) that a particular assemblage might have. Assemblages on the periphery of Georges Bank might be less susceptible to changes in species composition and relative abundance because their component species are less trophically linked. The Shallow assemblage, on the other hand, appears to be particularly vulnerable to fishing and perhaps interspecific interactions. This type of knowledge will be helpful for understanding changes in fish abundance and community structure and for effectively managing fishery systems in the future.

ACKNOWLEDGMENTS

We would like to dedicate this paper to the men and women of the Northeast Fisheries Center, Woods Hole, MA, for without their long-term plan-

ning and tireless efforts in collecting the data, it would have been impossible to complete this work. We thank E. Beals for providing such good advice and helping with analyses. We are grateful for the friendship and assistance of G. Kruse, T. Hayden, and W. Gabriel, who provided much inspiration over the span of the last several years. We would also like to thank B. Brown for his help, direction, and patience.

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OBSERVER EFFECT ON INCIDENTAL DOLPHIN MORTALITY IN THE EASTERN TROPICAL PACIFIC TUNA FISHERY

Bruce E. Wahlen[1] and Tim D. Smith[2]

ABSTRACT

Scientific observers placed aboard a sample of purse seine vessels collect data that are used to estimate the total number of dolphins killed incidentally in the eastern tropical Pacific tuna fishery. If the presence of these observers, who are not crew members, affects incidental kill levels, then the kill estimates will be biased. To test for the existence of such an observer effect, we compared dolphin kill data that had been recorded by observers who differed in levels of obtrusiveness according to their purposes for data collection. Some observers were placed on board primarily to collect data for estimating the total number of dolphins killed annually. Other observers collected data both for that purpose and for monitoring compliance with dolphin-release regulations. Our results confirm that the presence of an observer does affect dolphin kill. The primary effect is an increase in the proportion of sets with no dolphins killed, and a decrease in the proportion of sets with one to nine dolphins killed. While the magnitude of the effect of observers cannot be estimated from our data, estimates of total dolphin mortality based on data collected by the scientific observers are biased downward.

Schools of dolphins of several species, primarily *Stenella attenuata* and *S. longirostris*, have been used since the late 1950s by purse seine fishermen in the eastern tropical Pacific Ocean (ETP) to locate and catch yellowfin tuna, *Thunnus albacares*. Perrin (1969) described the process of deploying, or setting, the net around the tuna and dolphins, and then releasing the dolphins while retaining the tuna. Significant numbers of dolphins have been killed incidentally in this fishery by becoming entangled in the purse seines (Smith 1983).

The National Marine Fisheries Service (NMFS) and the Inter-American Tropical Tuna Commission (IATTC) place scientific observers who are not crew members aboard a sample of tuna purse seine vessels to collect data related to dolphin kill. Both the NMFS and IATTC have used the data collected by these scientific observers to estimate the total number of dolphins killed annually by the entire tuna purse seine fleet (Lo et al. 1982; Hammond and Tsai 1983).

Additionally, the NMFS uses these data to monitor dolphin kills relative to annual kill limits established for the U.S. registered fleet (Lo et al. 1982). Periodic estimates of the cumulative numbers of dolphins killed are compared with the annual limit. If the limit is exceeded, U.S. vessels must stop fishing on the affected populations for the remainder of the year.

Data collected by the NMFS observers have also been used to monitor compliance of vessel operators with dolphin-release regulations, including the release of all live dolphins from the net (Federal Register 1977, 1980). Until recently, data collected by an NMFS observer could be used as evidence to prosecute vessel operators for violations of these regulations.

Observer effects have been defined in a general context as measurement procedures which influence and thereby change the behavior of the subject (Johnson and Bolstad 1973, p. 38). Researchers have encountered such effects in a variety of empirical sciences, including psychology (Johnson and Bolstad 1973), social science (Webb et al. 1966, p. 18), and biology (Ricker 1975, p. 87).

We defined an observer effect on the number of dolphins killed as a differential in levels of dolphin kill between trips made with and without a scientific observer. The existence of such a differential would introduce a bias into estimates of the total number of dolphins killed (Smith 1983; Powers[3]). Large numbers of sets involving dolphins (dolphin sets) are made each year (Punsly 1983), so even a moderate observer effect could result in a substan-

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.
[2]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA; present address: Northeast Fisheries Center Woods Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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Manuscript accepted November 1984.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

tial bias in the estimates of annual dolphin kill.

Directly testing for the existence of an observer effect on dolphin kills would require comparison of covert observations with observations by NMFS and IATTC observers. Based on the large difference between the kill rate observed covertly by one crew member and the kill rates recorded by NMFS observers during other fishing trips made by the same operator and vessel, Smith (1983) speculated that a large observer effect existed. We investigated the significance of the difference in kill rates reported by Smith (1983) by grouping NMFS-observed trips into sequences of trips with common operator and vessel. A few of these sequences of NMFS-observed trips revealed between-trip kill rate differences as large or larger than in the sequence that included the covert observations.

The existence of an observer effect can be indirectly tested without relying on data from covert observers. Johnson and Bolstad (1973) established the existence of an observer effect by comparing measurements made by observers with various levels of obtrusiveness to the human subjects whose responses were being measured. They concluded that the differences in the responses measured by observers with different levels of obtrusiveness implied that the observer's presence had affected the subjects' behavior. They noted, however, that the magnitude of an observer effect cannot be estimated using this approach.

Following this indirect approach, we tested for the existence of an observer effect on the numbers of dolphins killed by comparing dolphin kill data collected by scientific observers who differed in their purposes of data collection, and hence, in their levels of obtrusiveness.

DATA

The scientific observers were placed aboard a random sample of U.S. registered tuna purse seine vessels (Lo et al. 1982). Assignment of an NMFS or IATTC observer to vessels in the sample was also made randomly, subject to the constraint that any vessel sampled twice within a calendar year would be accompanied by an NMFS observer on at most one trip (Table 1).

Information collected for each NMFS- or IATTC-sampled fishing trip included departure date and data pertaining to each set (such as set type, date, and location), and for dolphin sets, the number of dolphins killed. Data available to the authors from NMFS-sampled trips included all of this information. However, data available from IATTC-sampled trips did not include departure date, and set dates were available only to the quarter of the year.

While the data items collected by both types of scientific observer have been similar over the years, for NMFS observers the purposes of the data collection changed after March 1981. The primary purposes of data collection, as explained to each vessel operator at a placement meeting held prior to departure, were as follows: 1) On NMFS-sampled trips begun from 1978 through March 1981, data were collected for estimating the annual kill of dolphins and for monitoring compliance with dolphin-release regulations; 2) on NMFS-sampled trips begun after March 1981 through the end of 1982, the data were still used for estimating dolphin kills but were no longer used to monitor compliance with dolphin-release regulations[4]; 3) on all IATTC-sampled trips, since the inception of that sampling program in 1979, data were collected for estimating total kill but were never collected for monitoring compliance with dolphin-release regulations.

As described above, the data collected by both NMFS and IATTC observers to estimate total dolphin kill can be used by the NMFS to halt fishing by U.S. vessels on specific dolphin populations for the remainder of the year. The data collected before March 1981 by the NMFS observers for monitoring compliance with dolphin-release regulations, however, can be used by the NMFS as evidence to prosecute operators who failed to comply. Thus, the operators are likely to be more conscious of the presence of an observer who is collecting data both for estimating dolphin kill and for monitoring com-

[4]The change in data collection purposes of NMFS observers after March 1981 was prompted by a court order forbidding the NMFS from using data collected by observers for monitoring compliance with dolphin-release regulations. No NMFS observers were placed on fishing trips begun from 1983 through part of 1984 because of a subsequent court order forbidding placement of NMFS observers without a search warrant.

TABLE 1.—Number of observed fishing trips which made at least one dolphin set from 1978 through 1982, by observer type and year. NMFS totals are subdivided according to departure date of trips (previous year, Jan.-Mar., Apr.-Dec.) and exclude trips in which fishing gear research was conducted.

Observer type	1978	1979	1980	1981	1982
NMFS					
Previous year	5	4	3	3	7
Jan.-Mar.	44	33	15	7	13
Apr.-Dec.	56	32	28	28	18
Total	105	69	46	38	38
IATTC	0	31	57	58	44
Total	105	100	103	96	82

pliance with dolphin-release regulations than an observer who is collecting data only for estimating dolphin kill. That this is the case is implied by the constraint in the sampling procedure that any vessel sampled twice within a calendar year may be accompanied by an NMFS observer on at most one trip.

METHODS

We tested for the existence of an observer effect on dolphin kills by comparing the number of killed dolphins recorded by more obtrusive observers with the number recorded by less obtrusive observers. We considered observers who collected data both for estimating dolphin kill and for monitoring compliance with dolphin-release regulations to be more obtrusive to vessel operators than observers who collected data only for estimating dolphin kill. Thus, we compared kills recorded by (1a) NMFS observers before and after March 1981, and (1b) NMFS and IATTC observers before March 1981. As a control, we compared the number of killed dolphins recorded by observers of equal obtrusiveness. That is, we compared kills recorded by (2a) IATTC observers before and after March 1981, and (2b) NMFS and IATTC observers after March 1981.

The frequency distributions of numbers of dolphins killed were extremely skewed, with very long right tails (Fig . 1). Normality assumptions were violated so strongly by these skewed distributions that ANOVA tests for differences in means, particularly one-sided tests, would be difficult to interpret (Glass et al. 1972). Therefore, we tested for differences in the percent of dolphin sets in which no dolphins were killed (zero-kill sets). This percent relates directly to the regulation requiring release of all live dolphins, and is a dominant feature of the dolphin kill distributions.

When comparing frequency distributions, we entertained the null hypothesis of equality of percent zero-kill sets. When comparing observers of different obtrusiveness levels, we tested this hypothesis against a one-sided alternative that distributions from more obtrusive observers had a higher percent

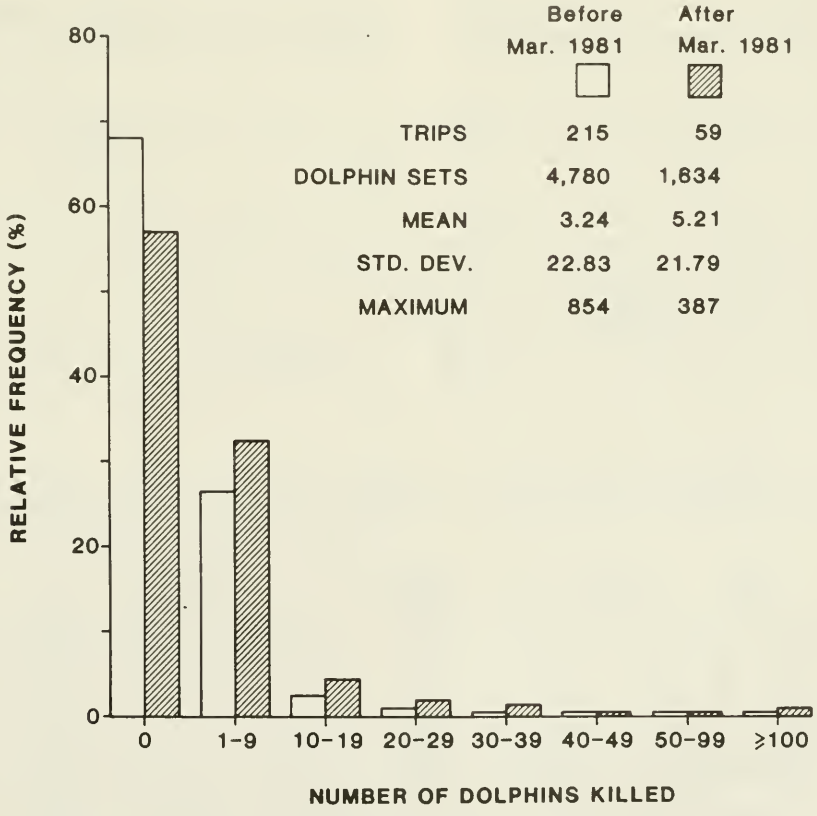

FIGURE 1.—Relative frequency distributions of number of dolphins killed incidentally during sets of NMFS-observed trips, 1978 through 1982, by trip departure date.

of zero-kill sets than distributions from less obtrusive observers. When comparing distributions from observers of equal obtrusiveness, we tested the null hypothesis against the two-sided alternate of inequality (Table 2). Results from all of our tests are reported at the 0.05 significance level.

TABLE 2.—Alternate hypotheses to the null hypothesis of equality of percent zero-kill sets for each of four comparisons, where Before and After refer to before or after March 1981. See text for details.

Comparison		Alternate hypothesis
1a.	NMFS before vs NMFS after	Before > After
2a.	IATTC before vs IATTC after	Before ≠ After
1b.	NMFS before vs IATTC before	NMFS > IATTC
2b.	NMFS after vs IATTC after	NMFS ≠ IATTC

For two-sided tests of differences in percents, we used the standard chi-square (χ^2) statistic with one degree of freedom (df). For one-sided tests, we used the square root of the chi-square statistic (Z), which is approximately normal (Snedecor and Cochran 1980, p. 126-127). In some instances, the expected cell frequencies were less than the traditionally accepted minimum of five. However, recent Monte Carlo results (Fienberg 1980, p. 172) suggest that the chi-squared distribution is an adequate approximation at the 0.05 significance level even when minimum expected values are as low as one.

While the sampling of vessels was nearly random, the actual sample obtained may not have been representative of factors affecting dolphin kills. It has been demonstrated that within the ETP, dolphin kills vary among three geographic areas[5] (Fig. 2) and by periods within the year (Lo et al. 1982). We divided the year into two periods: January-March and April-December. This division corresponds to the date of the change in data collection purposes of NMFS observers in 1981, and also tends to equalize sample size since vessels in this fishery are more active in the early part of the year.

We stratified the data by area and period of the year to account for biases due to possible nonrepresentativeness of the sample with respect to these two factors. When data on numbers of dolphins killed were available in all six area-period strata, we made overall two-sided tests for differences in per-

[5]K.-T. Tsai, Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92093, pers. commun. December 1983.

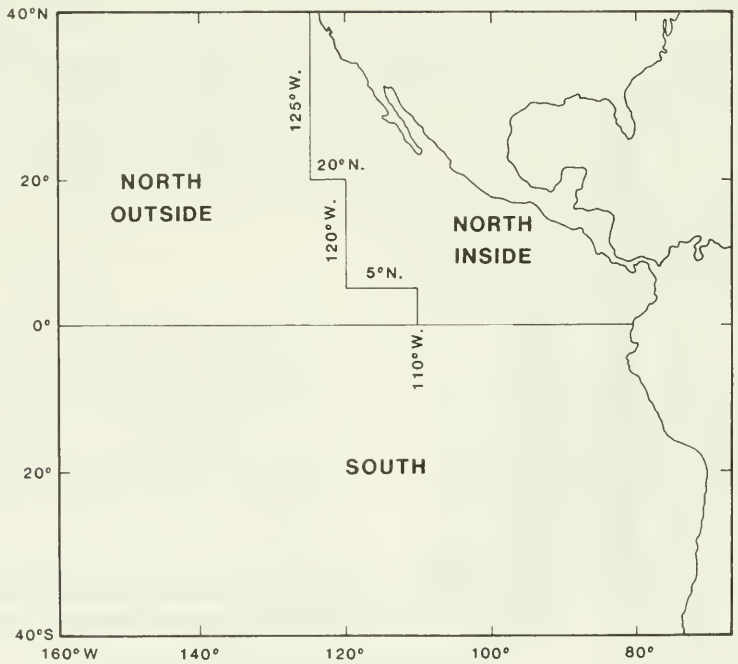

FIGURE 2.—The three areas of the eastern tropical Pacific used to stratify the data, bounded by lat. 40°N., long. 160°W., lat. 40°S., and the western coastline of the North and South American Continents.

cent zero-kill sets (conditional on period of the year and geographic area) by summing chi-square values and degrees of freedom from each stratum. When observations were not available in one of the strata, or when the alternative was one-sided, an overall test based on the chi-square statistic was not possible. In those cases, results of the tests within each stratum were considered separately.

RESULTS

The first two comparisons of frequency distributions test for differences in the percent of zero-kill sets in data collected by observers on trips begun before compared with trips begun after the change in NMFS observer data collection purposes in March 1981 (Comparisons 1a and 2a, Table 2). The last two comparisons test for differences in the percent of zero-kill sets in data collected by observers on trips begun during the same time period (Comparisons 1b and 2b, Table 2).

Before versus After

The percent of zero-kill sets for NMFS-observed trips was higher before March 1981 than after that date (Fig. 1), and within all area-period strata with complete data, the percent of zero-kill sets was larger before March 1981 (Table 3). The one-sided test of this difference (Comparison 1a, Table 2) was significant within four of the five area-period strata which had complete data, and was very nearly significant within the fifth (Table 3). Thus, the percent of zero-kill sets recorded by NMFS observers was significantly larger before March 1981.

The significant difference in percent of zero-kill sets for NMFS observers before compared with after March 1981 could be due to the change in data collection purposes of NMFS observers which occurred then. Alternatively, the difference could be due to a temporal decline begun before that date.

Allowing for period, the data prior to March 1981 do not show a pronounced trend for any of the three areas (Fig. 3). Although there appears to be a decline in the South for Period 2, this is unreliable as it depends entirely on the 1980 and 1981 data points representing a total of only 17 sets. Similarly, there seems to be a declining trend for the two northern areas. However, for the North Inside area the Period 1 points show no decline, and the possible decline of Period 2 points depends on the 1980 Period 2 point. A 95% confidence interval about this point (observed percent $\pm 2 \times$ standard error), however, is large relative to the difference between it and the Period 2 point of 1979. Further, any such declining trend in Period 2 points for the North Inside area is not reflected in the low 1978 point. A similar argument can be made for North Outside area data to reject the alternative explanation of the difference in percent zero-kill sets before and after March 1981 being the result of a temporal trend begun prior to March 1981.

That the differences in percent of zero-kill sets for NMFS-observed trips was not due to a temporal trend was also tested by comparing the percent of such sets for IATTC-observed trips before and after March 1981. The percent of zero-kill sets for IATTC-observed trips was higher before March 1981, but within the six area-period strata the differences were not consistent (Table 4). The two-sided test (Comparison 2a, Table 2) was significant within only one of the six area-period strata (Period 1, South), and the sample size within that stratum was very small (Table 4). The overall conditional test given area and period was not significant. Thus, IATTC-observed trips with dolphin sets from 1979 through 1982 did

TABLE 3.—Numbers of dolphin sets (n) made during NMFS-observed trips, 1978 through 1982. Sets are classified by trip departure date relative to March 1981 (before or after) and to period (1 = Jan.-Mar., 2 = Apr.-Dec.), by area of set (North Inside, North Outside, South), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (e), and the statistic Z are also tabulated. Values of $Z > 1.64$ are significant, as indicated by an asterisk.

		Period 1						Period 2							
		North Inside		North Outside		South		North Inside		North Outside		South		Total	
Kill		Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
0	n	1,498	226	0	21	107	0	972	421	591	229	86	33	3,254	930
	%	72.9	62.1	—	52.5	61.1	0.0	69.4	62.7	60.4	55.7	50.6	23.1	68.1	56.9
	e	1,464.7	259.3	0	21	104.0	3.0	941.9	451.1	577.4	242.6	64.6	54.4	—	—
>0	n	558	138	0	19	68	5	429	250	387	182	84	110	1,526	704
	%	27.1	37.9	—	47.5	38.9	100.0	30.6	37.3	39.6	44.3	49.4	76.9	31.9	43.1
	e	591.3	104.7	0	19	71.0	2.0	459.1	219.9	400.6	168.4	105.4	88.6	—	—
Total	n	2,056	364	0	40	175	5	1,401	671	978	411	170	143	4,780	1,634
	Z	4.18*		—		2.75*		3.01*		1.63		4.99*		—[1]	

[1]Computation of overall test statistic not possible because of one-sided alternative, and because of lack of data in one stratum (Period 1, North Outside).

532	528	978	527	403	346	143	326	364	345	NIS
0	534	0	263	0	181	0	270	40	141	NOS
45	64	75	92	55	14	0	3	5	140	S

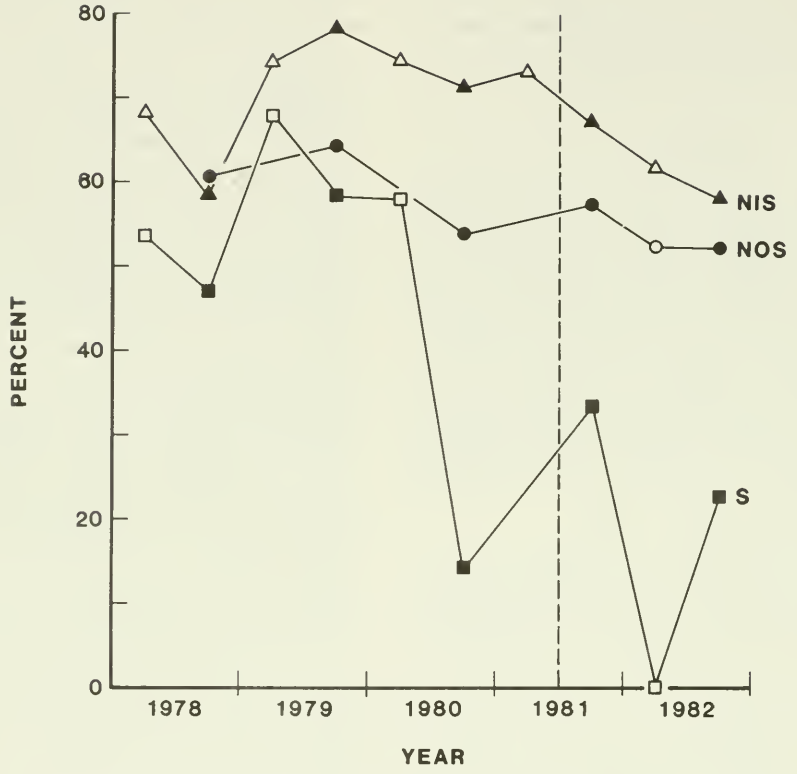

FIGURE 3.—Number of dolphin sets (upper portion) and percent of zero-kill dolphin sets (lower portion) for each of 3 areas (NIS = North Inside, NOS = North Outside, S = South) by period within year (open symbol = Jan.-Mar., closed symbol = Apr.-Dec.). Data are from NMFS-observed trips, 1978 through 1982. Vertical line separates data before and after March 1981.

TABLE 4.—Numbers of dolphin sets (*n*) made from 1979 through 1982, during IATTC-observed trips. Sets are classified by date of set relative to March 1981 (before or after) and to period (1 = Jan.-Mar., 2 = Apr.-Dec), by area of set (North Inside, North Outside, South), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (e), and the statistic χ^2 with degrees of freedom (df) are also tabulated. Values of $\chi^2 > 3.84$ (1 df) or 12.59 (6 df) are significant, as indicated by an asterisk.

		Period 1						Period 2							
		North Inside		North Outside		South		North Inside		North Outside		South		Total	
Kill		Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
0	*n*	537	188	9	3	13	3	709	721	291	328	5	35	1,564	1,278
	%	67.1	71.2	26.5	14.3	38.2	12.0	70.0	70.1	58.7	55.6	33.3	24.1	65.4	61.6
	e	545.1	179.9	7.4	4.6	9.2	6.8	709.8	720.2	282.7	336.3	3.8	36.2	—	—
>0	*n*	263	76	25	18	21	22	304	307	205	262	10	110	828	795
	%	32.9	28.8	73.5	85.7	61.8	88.0	30.0	29.9	41.3	44.4	66.7	75.9	34.6	38.4
	e	254.9	84.1	26.6	16.4	24.8	18.2	303.2	307.8	213.3	253.7	11.2	108.8	—	—
Total	*n*	800	264	34	21	34	25	1,013	1,028	496	590	15	145	2,392	2,073
	χ^2	1.53		1.13		5.02*		0.01		1.04		0.61		9.34	
	df	1		1		1		1		1		1		6	

not differ significantly in their percent of zero-kill sets before or after March 1981.

Same Time Period

Before March 1981 the percent of zero-kill sets was higher for NMFS-observed trips than for IATTC-observed trips (Fig. 4), and within all area-period strata with complete data, the percent of zero-kill sets was larger for the NMFS observers (Table 5). The one-sided test (Comparison 1b, Table 2) was significant within four of the five area-period strata which had complete data (Table 5). Thus, for trips making dolphin sets from 1979 through March 1981, NMFS observers recorded a significantly higher percent of zero-kill sets than did IATTC observers.

According to our hypothesis, the difference in percent of zero-kill sets between NMFS- and IATTC-observed trips before March 1981 should have disappeared after March 1981 when the purposes for data collection of NMFS observers became nearly the same as for IATTC observers. After March 1981 the percent of zero-kill sets was higher for IATTC-observed trips than for NMFS-observed trips (Fig. 5), but within the six area-period strata the differences were not consistent (Table 6). The two-sided test (Comparison 2b, Table 2) was significant within only one of the six area-period strata (Period 1, North Inside), yet this one chi-square statistic was so large that the overall conditional test for all six strata was also significant (Table 6). It is difficult to interpret the overall result in this situation because of the extraordinary influence of one stratum. However, after March 1981 the percent of zero-kill sets on NMFS-observed trips was clearly not higher than on IATTC-observed trips.

While one would expect the mean number of dolphins killed to decrease when the percent of zero-kill sets increases, this is not necessarily so because of the sensitivity of the mean of a sample to the maximum value in the sample. For instance, in Figure 4 the NMFS maximum is nearly twice that of the IATTC, resulting in a larger NMFS mean despite the higher percent of zero-kill sets in the NMFS sample.

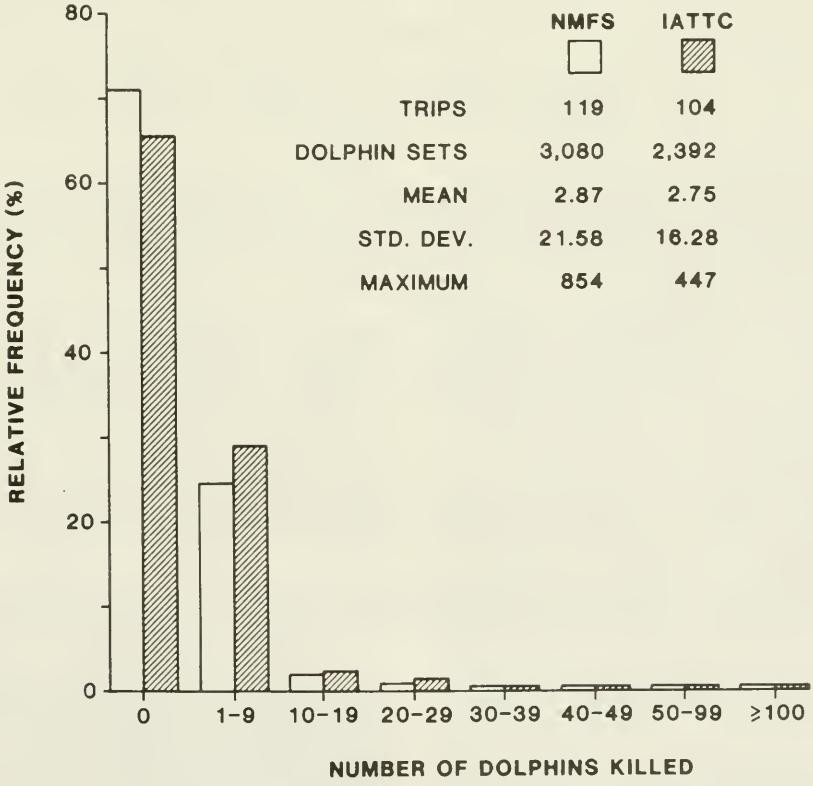

FIGURE 4.—Relative frequency distributions of number of dolphins killed incidentally during sets made from 1979 through March 1981, by observer type.

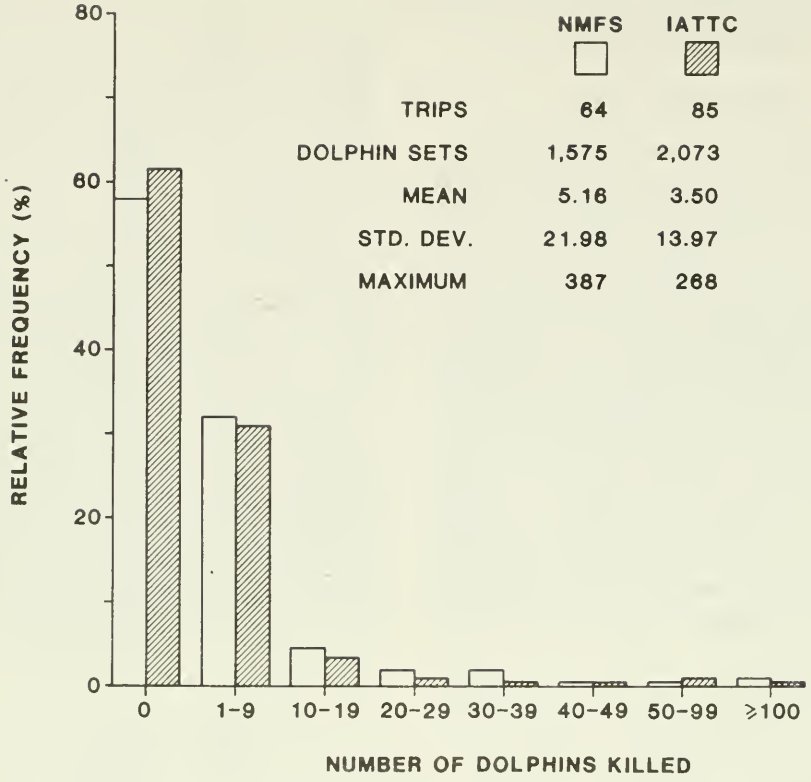

FIGURE 5.—Relative frequency distributions of number of dolphins killed incidentally during sets made after March 1981 through 1982, by observer type.

TABLE 5.—Numbers of dolphin sets (*n*) made from 1979 through March 1981. Sets are classified by observer type (NMFS, IATTC), by area of set (North Inside, North Outside, South), by date of set relative to period (1 = Jan.-Mar., 2 = Apr.-Dec.), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (e), and the statistic *Z* are also tabulated. Values of $Z > 1.64$ are significant, as indicated by an asterisk.

		Period 1						Period 2						Total	
		North Inside		North Outside		South		North Inside		North Outside		South			
Kill		NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC
0	*n*	820	537	0	9	96	13	942	709	267	291	62	5	2,187	1,564
	%	72.7	67.1	—	26.5	53.9	38.2	76.8	70.0	60.1	58.7	59.6	33.3	71.0	65.4
	e	793.9	563.1	0	9	91.5	17.5	904.0	747.0	263.6	294.4	58.6	8.4	—	—
>0	*n*	308	263	0	25	82	21	284	304	177	205	42	10	893	828
	%	27.3	32.9	—	73.5	46.1	61.8	23.2	30.0	39.9	41.3	40.4	66.7	29.0	34.6
	e	334.1	236.9	0	25	86.5	16.5	322.0	266.0	180.4	201.6	45.4	6.6	—	—
Total	*n*	1,128	800	0	34	178	34	1,226	1,013	444	496	104	15	3,080	2,392
	Z	2.64*		—		1.68*		3.66*		0.46		1.92*		—[1]	

[1]Computation of overall test statistic not possible because of one-sided alternative, and because of lack of data in one stratum (Period 1, North Outside).

DISCUSSION AND CONCLUSIONS

We established the existence of an observer effect on the number of dolphins killed incidentally in the ETP yellowfin tuna fishery by following two lines of argument. First, we demonstrated a decrease in the percent of sets with no dolphins killed on NMFS-observed trips after March 1981, when monitoring compliance with dolphin-release regulations was removed as a data collection purpose (Table 3). We further showed that this difference was not due to a temporal trend in fishing conditions by examin-

TABLE 6.—Numbers of dolphin sets (*n*) made from April 1981 through 1982. Sets are classified by observer type (NMFS, IATTC), by area of set (North Inside, North Outside, South), by date of set relative to period (1 = Jan.-Mar., 2 = Apr.-Dec.), and by numbers of dolphins killed (0, >0). Percents of column totals (%), expected frequencies (e), and the statistic χ^2 with degrees of freedom (df) are also tabulated. Values of $\chi^2 > 3.84$ (1 df) or 12.59 (6 df) are significant, as indicated by an asterisk.

		Period 1						Period 2							
		North Inside		North Outside		South		North Inside		North Outside		South		Total	
Kill		NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC	NMFS	IATTC
0	*n*	193	188	1	3	1	3	455	721	249	328	13	35	912	1,278
	%	55.6	71.2	14.3	14.3	10.0	12.0	66.4	70.1	56.1	55.6	15.9	24.1	57.9	61.6
	e	216.4	164.6	1.0	3.0	1.1	2.9	470.3	705.7	247.8	329.2	17.3	30.7	—	—
>0	*n*	154	76	6	18	9	22	230	307	195	262	69	110	663	795
	%	44.4	28.8	85.7	85.7	90.0	88.0	33.6	29.9	43.9	44.4	84.1	75.9	42.1	38.4
	e	130.6	99.4	6.0	18.0	8.9	22.1	214.7	322.3	196.2	260.8	64.7	114.3	—	—
Total	*n*	347	264	7	21	10	25	685	1,028	444	590	82	145	1,575	2,073
	χ^2	15.53*		0.00		0.03		2.63		0.02		2.16		20.37*	
	df	1		1		1		1		1		1		6	

ing the data by period (Fig. 3) and by demonstrating the lack of a corresponding change in data collected by IATTC observers (Table 4).

Second, we demonstrated that before March 1981 the percent of sets with no dolphins killed was higher for NMFS observers collecting data both for estimating dolphin kill and for monitoring compliance with dolphin-release regulations than for IATTC observers collecting data only for estimating dolphin kill (Table 5). To validate this comparison we also demonstrated that the difference disappeared, or perhaps was reversed, following March 1981 when monitoring compliance with dolphin-release regulations was removed from the NMFS observers' responsibilities (Table 6). Following Johnson and Bolstad (1973), these differences in the data collected by observers differing in their purposes of data collection, and hence in their obtrusiveness, imply the existence of an observer effect.

In making these comparisons, we stratified the data to account for possible differences in fishing conditions in different geographic areas and throughout the year because both area and time of year are important determinants of dolphin mortality. Thus, the differences in the percent of zero-kill sets which we identified cannot be attributed to nonrepresentativeness of the data with respect to area and time of year.

We did not attempt to test for other differences in the frequency distributions of kills, such as changes in the percent of moderate or large kill sets. Sets with large numbers of dolphins killed are rare, and are generally associated with unusual circumstances, such as mechanical failures. The percent of sets with 1-9 dolphins killed appears to vary inversely with the percent of sets with zero dolphins killed (Figs. 1, 4, 5).

Powers et al.[6] showed that the use of some dolphin-release procedures significantly reduces dolphin mortality. Thus, more time and effort expended by the operator on release of dolphins could result in an increase in the frequency of sets with no dolphins killed, and a corresponding decrease in the frequency of sets with 1-9 dolphins killed. A greater tendency for vessel operators to take the additional time in the presence of an observer collecting data for monitoring compliance with dolphin-release regulations could account for the differences we have demonstrated.

The significantly different relative frequency of zero-kill sets recorded by NMFS observers after March 1981 (Table 6) was not expected under our hypothesis. As noted above, this difference was localized to one area-period stratum, and the other five strata were consistent with the null hypothesis of no difference. Either this difference is merely a sampling anomaly, or there are differences between observers in more recent years that we have not taken into account.

Gulland (1983, p. 111) described a method of testing for the existence of a tagging effect that is analogous to our indirect method of testing for an observer effect. He suggested comparing the proportions of tags returned from fish tagged under poor and good conditions. In both Gulland's and our methods, the absolute magnitude of the effects cannot be estimated. For instance, in Gulland's example improvement in the conditions under which tags are applied is unlikely to eliminate entirely the tagging effect. Similarly, the reduction in observer ob-

[6]Powers, J. E., N. C. H. Lo, and B. E. Wahlen. 1979. A statistical analysis on effectiveness of porpoise rescue procedures in reducing incidental mortality. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-7, 29 p.

trusiveness after March 1981 is unlikely to have eliminated entirely the observer effect because the data collected by scientific observers after 1981 were still used to monitor dolphin kills relative to annual kill limits. Observers collecting data that could not be used for monitoring kill limits would be even less obtrusive than the scientific observers, and covert observers would be, of course, completely unobtrusive.

Based on our analysis, we would expect that the frequency of zero-kill sets would be lower on unobserved vessels than on vessels with a scientific observer. This lower frequency of zero-kill sets, coupled with an increased frequency of sets with 1-9 dolphins killed, suggests that the average kill rate on unobserved vessels would be higher. Estimates of total kill, based on the average kill rates from the scientific observers, would therefore be underestimated.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance of M. M. Croom in providing data and in early discussions of the problem. We also acknowledge the assistance of K. E. Wallace and J. S. Cole in providing data. We are indebted to D. G. Chapman and W. F. Perrin for suggesting analytical methods. We also appreciate the helpful reviews by F. G. Alverson, I. Barrett, P. S. Hammond, R. S. Holt, N. C. H. Lo, N. A. Mendes, J. M. Michalski, G. T. Sakagawa, and K.-T. Tsai, as well as the reveiws by two anonymous individuals.

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FOOD HABITS OF JUVENILE ROCKFISHES (*SEBASTES*) IN A CENTRAL CALIFORNIA KELP FOREST

MICHAEL M. SINGER[1]

ABSTRACT

The diets and feeding morphology of juveniles of seven rockfish species (Scorpaenidae: *Sebastes*) were investigated in a kelp forest at Stillwater Cove, Carmel Bay, CA. The seven species could be divided into two groups, those which fed primarily on open water prey in the water column and those which fed on substrate-associated prey. Substrate-associated prey were generally larger than open water prey and were eaten by predators with relatively larger heads and mouths and shorter gill rakers. Comparison of juvenile diets and foraging patterns with those of adults showed that both foraged in similar manners and in the same general habitats. The absence of aggressive interactions within or among species and high intraspecific variability of foraging patterns suggests that little interference or exploitative competition was present.

Most of the literature on rockfishes deals mainly with aspects of either adult or larval biology (DeLacey et al. 1964; Phillips 1964; Miller and Geibel 1973; Westrheim 1975; Larson 1980a, b, c). Little of this literature deals with the juvenile stage. Juvenile rockfishes often use nearshore kelp beds as nursery grounds and, during certain times of the year, are the most abundant members of the kelp-forest fish community (Burge and Schultz 1973). The change from pelagic life to a nearshore, reef-dwelling existence represents a major ecological transition. With so many juvenile rockfish species co-occurring in kelp forests, the potential for competitive interaction is great. Gaining an understanding of these fishes' patterns of resource utilization (e.g., food or space) may be important in assessing the mechanisms that affect their survival.

The purpose of this study was threefold: 1) to investigate the food habits of juvenile rockfishes occurring in a nearshore kelp forest, 2) to determine the extent to which diet differed within and among the various species present, and 3) to compare the relationship between diet and morphology in juvenile and adult forms.

The juveniles of seven rockfish species were studied. The adults of six of these species usually occur nearshore, in association with rock reefs: blue rockfish, *S. mystinus*; black rockfish, *S. melanops*; olive rockfish, *S. serranoides*; copper rockfish, *S. caurinus*; gopher rockfish, *S. carnatus*; and kelp rockfish, *S. atrovirens* (Hallacher 1977; Roberts 1979). Adults of the seventh species, the canary rockfish, *S. pinniger*, occur deeper and usually offshore (Miller and Lea 1972). For purposes of this study, an individual was designated a juvenile upon first appearance in the kelp forest, where fish were usually 25 to 30 mm SL. The fish used in this study generally ranged from 30 to 70 mm SL.

Sebastes mystinus and *S. pinniger* are among the earliest species to recruit, usually appearing as early as April. *Sebastes mystinus* usually occurs in the water column above 6 m while *S. pinniger* occurs on the substrate usually near sand/rock interfaces. *Sebastes caurinus* begins recruiting around late April or May and is found initially among kelp fronds and near the surface. Next to arrive are *S. serranoides* and *S. melanops* which first appear in May and June. Both these species occur mostly in the midwater within the kelp forest. *Sebastes carnatus* usually begins to recruit in late June and July and, like *S. caurinus*, is found initially among kelp fronds at the surface. Both *S. caurinus* and *S. carnatus* move down from the canopy and take positions near the bottom after a couple of months (around June or July for *S. caurinus* and late August or September for *S. carnatus*). The last of these species to recruit is *S. atrovirens*, which begins to appear in late July and August and occurs in the surface kelp canopy.

METHODS AND MATERIALS

Study Site

All observations and samples were taken between

[1]Moss Landing Marine Laboratories, Moss Landing, CA; present address: VANTUNA Research Group, Occidental College, Moore Laboratory of Zoology, 1600 Campus Road, Los Angeles, CA 90041.

Manuscript accepted November 1984.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

May 1980 to October 1981 at a rock reef at Arrowhead Point in Stillwater Cove, Carmel Bay, CA (about lat. 36°33.6'N, long. 121°56.3'W). Bottom depths at the study site averaged about 12.5 m below MLLW (mean low low water). The reef was roughly triangular, bounded by sand flats which sloped into deeper water on all but the nearshore side (Fig. 1). The reef substrate was composed of both high and low relief basaltic rock interspersed with areas of coarse, granitic sand and a few patches of worm tubes (*Diopatra* sp.). Stillwater Cove is protected from the prevailing north and northwest swells and winds. However, it is exposed to the most severe southerly storms which commonly occur from October to February.

The rock substrate was covered with an extensive mat of coralline algae and sessile invertebrates. The dominant algal form was the giant kelp, *Macrocystis pyrifera*, which became very thick in the summer months and represented a major structural component of the reef. Except for corallines, understory algae (*Pterogophora californica*, *Cystoseira osmundacea*, and seasonally dense patches of *Desmarestia ligulata*) were relatively sparse and patchy. *Desmarestia* abundance increased in the fall as the surface kelp canopy decreased. Drift algae of several types entered the reef at times and often became a major microhabitat. It usually occurred along the sand/rock interface or in low patches in the interior of the reef.

Field Collections

All fish used for stomach content analysis were collected with a 1 m × 1 m × 1.5 m opening-closing, diver-held net. The net was constructed of 1/8-in stretch-mesh nylon netting on a 1/4-in PVC frame mouth. The mouth of the net was hinged in the middle with tygon tubing. This allowed easy operation by a single diver in close spaces. Collected fish were brought to the surface and the stomachs injected with 10% Formalin[2]. The fish were then preserved whole in 10% Formalin, then washed in freshwater, and stored in 70% ethanol.

The majority of fish collected for gut analysis were taken from June to August of both 1980 and 1981 with some supplemental collections occurring in October and November of 1980. Collections were made during both day and night.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Laboratory Methods

Each fish was blotted dry and weighed to the nearest 0.01 g. The entire visceral mass was removed, and the stomach and intestine were then separated from the remaining viscera. The contents of each stomach were emptied into a small dish and examined under a binocular dissecting scope. Food items were separated by general taxonomic category (e.g., calanoid copepods, zoea larvae, mysid shrimp, etc.). These general categories were used because not all prey items found were in good enough condition to identify to species, thus identifying some items further than others could be misleading. Each category was enumerated by number and percent volume. The percent of the total stomach volume of each prey type was estimated by spreading the contents to a uniform thickness over a background grid and then estimating the area represented by each type. Since contents were spread to an equal thickness, area and volume were considered directly proportional. Digestive state of contents was estimated on a subjective one to five scale (DeWitt and Cailliet 1972). In addition, a subset of each prey type was taken from stomach contents and measured along its longest axis to the nearest 0.005 mm using an ocular micrometer for later estimation of mean sizes of each prey type.

Analytical Methods

A plot of cumulative number of prey types against randomly pooled number of stomachs was constructed for each species in order to assess adequacy of sample sizes. An asymptotic leveling of this type of plot indicates a sufficient sample size. The mean percent by estimated volume (%V) and by number (%N) of each prey type were calculated for each fish species as an average of all values for individual specimens. The mean frequency of occurence (%FO) was also calculated for each prey type in each predator as the number of times the prey type was seen divided by the total of stomachs examined. The importance of each prey type was calculated using the index of relative importance (IRI) described by Pinkas et al. (1971). The IRI used the proportion by amount (%N), volume (%V), and occurrence (%FO) of each prey type (IRI = (%N + %V) × %FO). The diets of the seven species studied were compared using the percent similarity index (PSI) (Whittaker 1952): $PSI = 1 - 0.5 \Sigma pih - pjh$. Where pi and pj are the proportions by IRI of each prey type (h) in the two predators being compared. In calculating

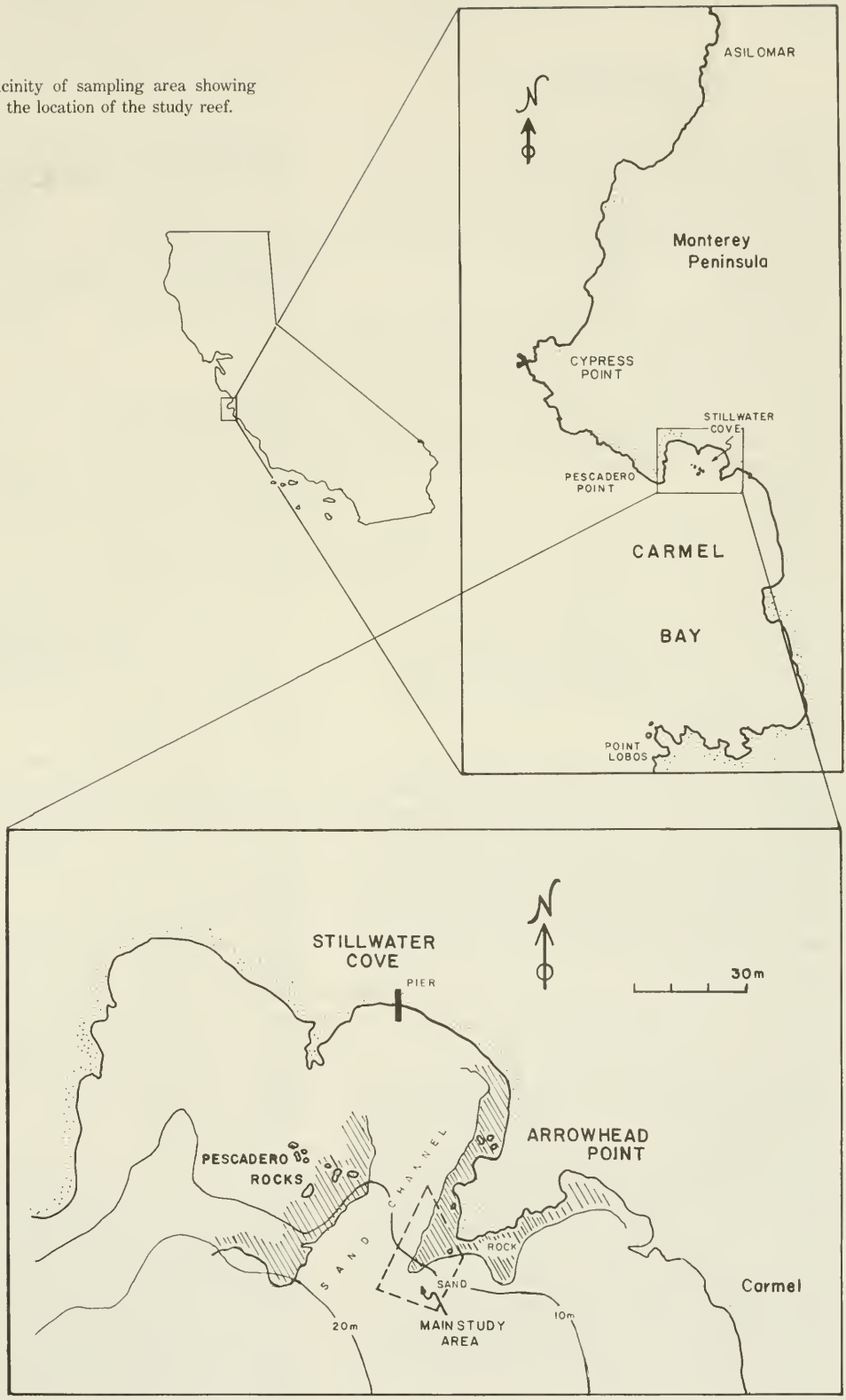

FIGURE 1.—Map of vicinity of sampling area showing Stillwater Cove and the location of the study reef.

overlap values %IRI values were used as the proportion, p.

Morphological Comparison

Several measurements were taken on a subsample of fish of each species covering all sizes encountered in this study. These included standard length, head length, and gape. Mean length of the five gill rakers nearest the angle on the ventral limb of the first gill arch, and the gap between them, were also measured.

The feeding related morphological characteristics chosen for statistical comparison were head length, gape, gill raker length, and gill raker spacing. Gape and gill raker spacing were compared as absolute measurements. Gill raker lengths were standardized to a proportion of head length and head length was standardized as a proportion of standard length for comparison.

Gape was compared using a one-way analysis of covariance (ANCOVA). This analysis regressed the natural log of the gape against the natural log of fish standard length to allow comparison over a range of fish sizes and to achieve linearity (Sokal and Rohlf 1969; Chen 1971). Relative head length, gill raker spacing, and relative gill raker length were compared among species with a Model I, one-way analysis of variance (ANOVA).

Multiple range comparisons were then made between individual species to detect groupings. Regression lines resulting from the ANCOVA were subjected to Newman-Keuls pairwise comparisons. Mean values obtained from ANOVAs were subjected to Student-Newman-Keuls (SNK) multiple range tests. All statistical procedures used followed those presented in Sokal and Rohlf (1969) and Snedecor and Cochran (1980).

Prey Abundance

Qualitative assessment of prey abundances was made from zooplankton tows done in the kelp forest. A standard 0.5 m diameter net with 0.333 μm mesh was used. Tows were done in sets of three, 3 min each: one within 0.5 m of the canopy, one in midwater, and one within 0.5 m of the bottom. These were done during both day and night. Generally, only presence or absence of plankton types was noted, along with relative daytime vs. nightime differences in abundances. Absolute abundances were not estimated. Zooplankton samples were taken once in mid-June 1980 and once in mid-July 1981. A total of 12 samples were collected.

RESULTS

A total of 265 juveniles of the seven species was examined for stomach content analysis: 27 *S. melanops* (53 to 67 mm SL, $\bar{x}$ = 57.9); 51 *S. serranoides* (44 to 63 mm; $\bar{x}$ = 51.8); 63 *S. pinniger* (28 to 56 mm, $\bar{x}$ = 43.7); 23 *S. mystinus* (46 to 72 mm, $\bar{x}$ = 59.1); 38 *S. atrovirens* (38 to 64 mm, $\bar{x}$ = 47.1); 42 *S. caurinus* (35 to 62 mm, $\bar{x}$ = 48.7); and 21 *S. carnatus* (33 to 65 mm, $\bar{x}$ = 44.4). An often co-occuring cogener of *S. carnatus*, *S. chrysomelas*, was not found during this study.

Diet Analysis

The cumulative prey type curves versus number of stomachs examined leveled off asymptotically, indicating that sample sizes for all species were sufficient to characterize their food arrays. All species were found to be zooplanktivores, consuming both open water and substrate-associated prey. Open water prey, which mainly float free in the water column, consisted mostly of juvenile copepods, zoea, and juvenile spionid polychaetes, while substrate-associated prey, which were generally found directly associated (<0.5 m away) with a physical structure (rock, kelp, etc.), consisted mainly of gammarid amphipods, mysid and caridean shrimp, and two species of isopod (Table 1).

A wide variety of prey sizes were encountered (Table 2). Prey found in open water, such as calanoid and harpacticoid copepods, zoea, and larvaceans, were mostly < 1 mm in length, whereas substrate-associated prey, such as amphipods and decapods, were 3 to 4 mm or larger.

Mean number of prey items and prey taxa per individual were highly variable within and among species (Table 3). As would be expected, species which fed on small open water prey had higher numbers of prey per stomach. Conversely, those species which fed on large substrate-associated prey, which were often large enough to fill a stomach with a single prey item, had much lower numbers of prey items per stomach.

Sebastes mystinus fed mainly on the larvacean *Oikopleura* sp., with high occurrence of copepods, zoea, and juvenile polychaetes (Fig. 2). They had the most cosmopolitan diet and the highest intraspecific variability of prey types (a mean of almost six different prey types per individual) (Table 3). Because its diet was composed mainly of small open water prey, this species also had the highest mean number of prey items per individual.

Sebastes serranoides and *S. melanops* had very

TABLE 1.—Taxa of prey identified in the stomachs of juvenile rockfish; names in all-capitals are categories used in stomach content analysis. (?) signifies incomplete or unsure identification. Microhabitat associations: OW = open water prey, S = substrate oriented prey.

Prey type			Open water or substrate association
Algae			
Mostly reproductive *Cystociera osmundacea*			S
Occasional pieces of *Macrocystis* fronds			
Invertebrates			
Molluscs	- *Macoma* sp.		S
Copepods	- CALANOIDS: unidentified juveniles		OW
	HARPACTICOIDS: unidentified juveniles		OW/S
OSTRACODS	- Unidentified		OW
POLYCHAETES	- larval/juvenile Spionidae		OW
Cirripidea	- unidentified BARNACLE LARVAE		OW
ISOPODS	- *Dimonella globera*; *Idothea resicata*		S
Amphipods	- GAMMARIDS:	*Aoroides columbiana*	S
		Ampithoe sp.	
		Batea transversa	
		Najna kitmata (?)	
	CAPRELLIDS:	*Caprella* sp.	S
		Unidentified Protocerid	
	HYPERIIDS:	Unidentified	S
MYSIDS	- *Acanthomysis* sp.; *Neomysis* sp.		S
Decapods	- SHRIMP:	*Heptocarpus* sp.	S
		Hippolyte sp. (?)	
	ZOEA LARVAE: unidentified decapods and brachyurans		OW
	ANOMURANS: unidentified JUVENILE HERMIT CRAB		S
Larvaceans	- *Oikopleura* sp.		OW
FISH			
unidentified hard parts			S
unidentified fish eggs			OW

TABLE 2.—Mean (±95% confidence interval) sizes of individuals of the nine major prey types of juvenile rockfishes. Measured items were taken from stomach samples.

Species	Size (mm)		
	N	$\bar{x}$	95% C.I.
Open water prey			
Oikopleura sp.	50	0.69	0.04
Harpacticoid copepods	50	0.88	0.05
Calanoid copepods	50	0.96	0.03
Juvenile polychaetes	35	1.47	0.71
Zoea larvae	50	1.63	0.11
Substrate-associated prey			
Mysids	35	3.48	1.16
Gammarid amphipods	35	4.01	0.77
Isopods	30	4.29	0.89
Caridean shrimp	30	13.95	1.47

similar diets (Fig. 2, Table 4). Both species ate mainly open water prey: calanoid copepods, harpacticoid copepods, and zoea larvae in order of importance. These species also showed fairly high intraspecific diet variability—5.3 and 4.4 prey taxa per individual for *melanops* and *serranoides*, respectively.

The two species which showed major microhabitat shifts (Carr 1983), *S. caurinus* and *S. carnatus*, also showed large dietary changes. While in the canopy (generally <45 mm in SL), *S. caurinus* ate predominantly calanoid copepods, with harpacticoids and zoea also eaten fairly consistently (Fig. 2). However, after moving out of the canopy and down to the bottom near kelp stipes and rocks, its diet shifted to primarily caridean shrimp, with gammarid amphipods being the second most important prey (Fig. 2). *Sebastes carnatus* showed much the same type of dietary shift accompanying its large habitat shift. While in the canopy, smaller *S. carnatus* ate nearly exclusively calanoid copepods (92% of the diet), while large individuals, which were found on the bottom, fed on caridean and mysid shrimp and isopods (Fig. 2). This marked change in diet can also be seen in Table 4. Within each of these species, the diet similarity between size classes was low. However, similarities between the two species within each size class was quite high.

Sebastes atrovirens was found in the kelp canopy and among kelp throughout all depths during the entire study (Carr 1983). This species fed mainly on gammarid amphipods, with calanoid and harpacticoid copepods and mysid shrimp also being very

TABLE 3.—Mean (±95% confidence interval) number of prey items and prey taxa per stomach and total number of prey types for the seven species of juvenile rockfishes.

Species	Items			Taxa		S
	N	$\bar{x}$	95% C.I.	$\bar{x}$	95% C.I.	Total
Open water predators						
Sebastes mystinus	23	142.6	74.9	5.8	0.4	13
S. caurinus (<45 mm)	17	136.4	64.7	3.4	0.7	8
S. carnatus (<45 mm)	12	101.4	79.6	1.9	0.7	5
S. serranoides	50	100.2	33.5	4.4	1.7	9
S. melanops	27	87.0	31.2	5.3	2.3	8
Substrate-oriented predators						
S. pinniger	59	35.5	18.3	4.3	1.6	15
S. atrovirens	33	34.9	20.3	2.2	0.4	8
S. caurinus (>45 mm)	21	2.5	1.3	1.5	0.3	9
S. carnatus (>45 mm)	11	2.3	1.2	1.6	0.7	5

TABLE 4.—Percent similarity (PSI) overlap values of juvenile rockfish diets. Proportions used for calculations are %IRI.

	serranoides	*melanops*	*mystinus*	*caurinus* <45 mm	*carnatus* <45 mm	*pinniger*	*atrovirens*	*caurinus* >45 mm	*carnatus* >45 mm
Sebastes serranoides	—	0.787	0.455	0.874	0.602	0.653	0.389	0.091	0.090
S. melanops		—	0.402	0.732	0.516	0.734	0.318	0.094	0.019
S. mystinus			—	0.384	0.127	0.458	0.239	0.097	0.043
S. caurinus (<45 mm)				—	0.668	0.573	0.427	0.185	0.204
S. carnatus (<45 mm)					—	0.297	0.259	0.043	0.034
S. pinniger						—	0.468	0.174	0.169
S. atrovirens							—	0.218	0.258
S. caurinus (>45 mm)								—	0.634
S. carnatus (>45 mm)									—

important in their diet (Fig. 2). Thus, this species' diet was similar to most other species (Table 4).

Sebastes pinniger had a very diverse diet (highest number of overall prey taxa found; Table 3). Individuals were found mainly over sand areas and the sand/rock interface at the edge of the kelp forest, generally within a few meters of the bottom. This species' diet consisted mainly of copepods and zoea larvae (open water prey), but gammarid amphipods and mysid shrimp (substrate-associated prey) were also important (Fig. 2).

Figure 2 shows that these seven species can be split into two basic categories: open water and substrate-associated predators (this categorization can also be seen in microhabitat differences [Carr 1983]). Open water predators—*S. melanops*, *S. mystinus*, *S. serranoides*, and small *S. caurinus* and *S. carnatus*—are those that ate mainly copepods and zoea larvae. Substrate-oriented predators—*S. atrovirens* and larger *S. caurinus* and *S. carnatus*—are those that ate predominantly amphipods and decapods. *Sebastes pinniger* is intermediate between these categories. Its microhabitat and behavior are that of a substrate-associated predator, but its diet is more similar to the open water predators (Table 4).

Prey Distribution

Midwater organisms such as copepods, zoea larvae, and polychaetes were very abundant in all parts of the water column. Calanoid copepods were the most abundant type during the day at all depths, while both calanoids and harpacticoids were very abundant at night. Amphipods, mysids, caridean shrimp, and isopods were very abundant in and around all substrate types (kelp canopy, stipes, rocks, and drift algae). Isopods and amphipods were most abundant in the canopy and stipes, while amphipods, mysids, and carideans were more often abundant near rock and drift algae and around kelp holdfasts. These invertebrates remained near substrate during the day, moving farther away at night.

Morphological Comparisons

ANOVAs of relative head length, relative gill raker length, and gill raker spacing among species were all significant at the $P < 0.001$ level (Table 5). Generally, the open water and substrate-associated classifications also held true for groupings by morphology.

In general, open water predators had smaller heads and larger gill rakers. *Sebastes mystinus*, *S.*

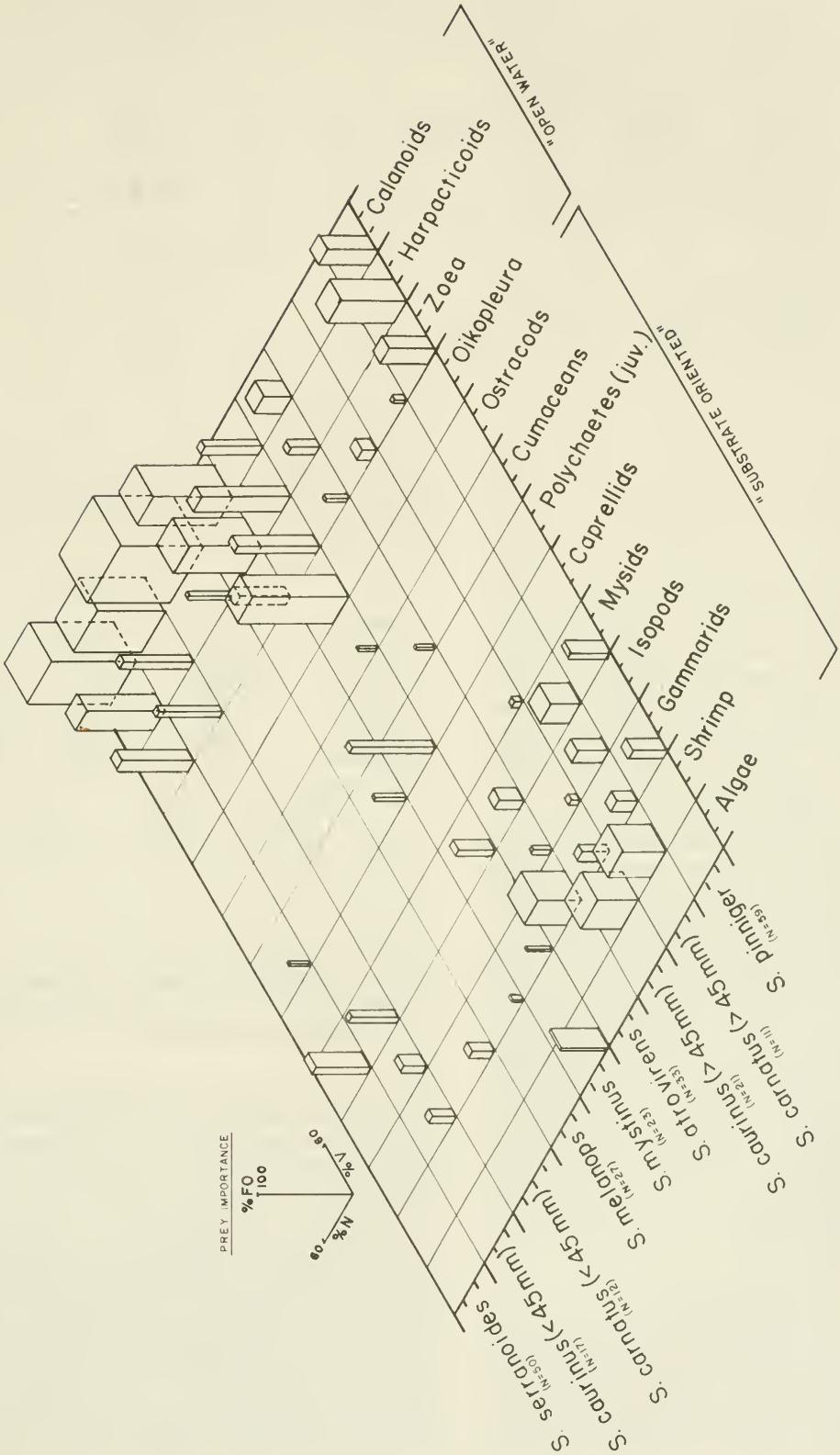

FIGURE 2.—Three dimensional trophic spectrum of juvenile rockfish diets. %N and %V are the horizontal axes with %FO on the vertical axis. Size of each box is equivalent to each prey type's importance.

TABLE 5.—Results of Student-Newman-Keuls multiple range comparisons on head length and gill raker length and spacing of juvenile rockfishes (*Sebastes*). Numbers in parentheses are significance levels of analyses of variance (ANOVA).

Relative head length ($P < 0.0001$)
Groupings at $\alpha = 0.05$ level (mean head lengths)

mystinus	*serranoides*	*melanops*	*atrovirens*	*caurinus*	*pinniger*	*carnatus*
0.3368	0.3620	0.3660	0.3808	0.3882	0.3890	0.3908

Relative gill raker length ($P < 0.001$)
Groupings at $\alpha = 0.05$ level (mean raker lengths)

carnatus	*caurinus*	*atrovirens*	*serranoides*	*pinniger*	*mystinus*	*melanops*
0.1008	0.1070	0.1165	0.1185	0.1222	0.1296	0.1322

Gill raker spacing ($P < 0.001$)
Groupings at $\alpha = 0.05$ level (mean spacing)

pinniger	*melanops*	*atrovirens*	*carnatus*	*mystinus*	*caurinus*	*serranoides*
0.226	0.234	0.238	0.248	0.262	0.312	0.316

serranoides, and *S. melanops*, which all have relatively long, slender bodies, had significantly smaller heads than *S. caurinus*, *S. carnatus*, and *S. pinniger* (Table 5). *Sebastes mystinus* and *S. melanops* also had significantly longer gill rakers than *S. caurinus* and *S. carnatus*, with *S. serranoides* having intermediate length rakers. *Sebastes atrovirens* was relatively intermediate in both measurements, but tended to be more like the predators with larger heads and shorter gill rakers. Groupings for gill raker spacing were less distinct. The open water/substrate-associated classifications also broke down with this measurement. *Sebastes pinniger*, *melanops*, and *atrovirens* had more closely spaced rakers, while *S. caurinus* and *serranoides* had the widest spaced rakers. *Sebastes mystinus* had an intermediate value (Table 5). Regression lines obtained from the ANCOVA showed that gape grew isometrically with length in all seven species, but that there were significant differences in the size of gape relative to body size among the species (Table 6). The slopes of the lines of ln (gape) on ln (SL) were all statistically indistinguishable from unity, but the intercepts did show a significant difference ($P < 0.001$, ANCOVA). Much of this significant difference was likely due to *S. caurinus*, which had a much larger mouth than the other species. *Sebastes serranoides* also had a fairly large mouth. All other species had very similar-sized mouths (Table 6).

TABLE 6.—Results of the one way analysis of covariance (ANCOVA) performed on regressions of ln (gape) versus ln (SL) of juvenile rockfishes.

Regression statistics

Species	Slope	Intercept	*r*
Sebastes caurinus	0.6745	−0.4173	0.8259
S. serranoides	0.8332	−1.2024	0.8363
S. pinniger	0.9876	−1.6759	0.9640
S. melanops	0.9761	−1.7070	0.9614
S. mystinus	0.9555	−1.7470	0.9224
S. carnatus	1.0482	−1.8439	0.9652
S. atrovirens	1.0561	−2.0053	0.9661

ANCOVA statistics

	MSnum	df	MSdenom	df	*F*	*P*
Slope	0.01	7	0.0057	155	1.76	NS
Intercept	0.16	6	0.039	161	40.68	$P < 0.001$

DISCUSSION

Many species of fish change diet as they grow (Ross 1978; MacPherson 1981). This may be because of changes in habitat, thus changing available food sources, or it may simply be a functional response to changes in fish size and/or metabolic needs. Although there are dietary differences between the juveniles and adults of the species studied here, their foraging patterns and habitats are very much the same.

Species who were water column feeders as juveniles remain water column feeders as adults. Juvenile *S. serranoides* ate primarily copepods and zoea larvae (Hobson and Chess 1976; this study). Adults also feed in the water column, eating primarily small fish and euphausiids (Love 1978). Juvenile *S. melanops* fed in the open water (on copepods), as do the adults, which eat small fish, euphausiids, and polychaetes (Hallacher 1978; Roberts 1979). This trend also holds for *S. mystinus*. Juveniles foraged in the water column, mostly on *Oikopleura* and copepods. Adults also aggregate and feed in the open water, but eat mostly tunicates and crustaceans (Hallacher 1977; Roberts 1979).

The ontogenetic similarity in foraging was also seen in substrate-oriented feeders. Juvenile *S. atrovirens* ate mostly large, demersal, gammarid amphipods. However, copepods ranked second in their diet, presumably because of small individuals feeding in the open water below the kelp canopy. Adults of this species feed on amphipods, shrimp, and crabs which can be either demersal or free swimming (Quast 1968; Hobson and Chess 1976; Roberts 1979). Small juvenile *S. caurinus* and *S. carnatus* fed in the open water, while larger juveniles foraged demersally. The adults of these species also feed demersally. *Sebastes carnatus* is known to eat juvenile rockfish, ophiuroids, and crustaceans (Hallacher 1977; Roberts 1979), while adult *S. caurinus* eat mostly brachyurans and shrimp (Prince 1975; Prince and Gotshall 1976). Juveniles also seem to exhibit the same microhabitat preference as adults. *Sebastes serranoides*, *mystinus*, and *melanops* were found mainly in the midwater, while *S. caurinus*, *carnatus*, and *atrovirens* were generally seen to associate more closely with some physical substrate (kelp plants, rocks, etc.) (Carr 1983; pers. obs.). Thus, in these species it seems that once an individual has survived its life as a pelagic larva and entered the kelp forest, it assumes the general habitat and foraging characteristics of an adult.

Sebastes pinniger was the only species which showed different foraging patterns between juveniles and adults. Juvenile *S. pinniger* were generally found close to the bottom over sand or in association with the rock/sand interface at the edge of the reef (Carr 1983; pers. obs.) while adults occur higher in the water column in deep water offshore. Juveniles fed demersally on copepods over sand and drift algae very near the kelp forest. Adults feed in the water column on euphausiids and small fish (Phillips 1964). Recently, adults have been found to be more demersal feeders than other offshore rockfish (Brodeur 1982).

In assessing the mechanisms which might lead to the observed diet differences, several factors must be considered, such as prey distribution and abundance, prey availability, predator morphology, prey and predator activity patterns, and predator distribution.

Qualitative analysis of plankton samples, combined with underwater observations, showed that plankton were very abundant. Although the diel behavior patterns of shallow, inshore zooplankton are highly variable with respect to specific habitats, species, seasons, and latitudes, the patterns of plankton distribution observed were quite comparable with reported accounts in kelp forests (Hobson and Chess 1976; Coyer 1979; Hammer 1981).

Predator morphology is an important factor determining prey size in planktivorous fish. Certain features distinguish water column foraging fish, such as long, slender bodies, sharp head profiles, fine dentition on jaws and pharyngeal bones, and long, closely spaced gill rakers (Yasuda 1960; Davis and Birdsong 1973). Of the seven species studied, the water column feeders—*S. mystinus*, *S. serranoides*, and *S. melanops*—had smaller heads with longer gill rakers.

Water column foragers and substrate-associated foragers could be separated by both morphology and prey size. The water column foragers—*S. mystinus*, *S. serranoides*, and *S. melanops*—all had relatively long, slender bodies, small heads, and long gill rakers. This agrees with predictions, especially since the adults of these species are also water column foragers. Water column feeders also ate substantially smaller prey than did substrate predators (see Figure 2, Table 2). The substrate-associated feeders—*S. caurinus*, *S. carnatus*, and *S. atrovirens*, which ate larger prey—all had stouter bodies, larger heads, and shorter, less ornamented gill rakers.

Juveniles of *S. pinniger* were somewhat intermediate in feeding morphology. Their heads were large and stout, indicative of substrate-oriented feeding. However, they had long, thin bodies and long, fairly closely spaced gill rakers, which is indicative of water column foraging, as is displayed by adults. This intermediate situation may be indicative of the fact that *S. pinniger* may go through a second ecological transition from a reef-dwelling, substrate-associated juvenile form back to a more pelagic offshore situation as an adult.

Differing diel patterns can be one way for co-occurring predators to exploit similar resources while keeping interspecific interactions low (Keast and Webb 1966; Schoener 1974; Bray and Ebeling 1975). In zooplanktivores diel patterns of both predators and prey are important (Hobson and Chess 1976; Robertson and Howard 1978). Most juveniles were active only during the day, with the possible exceptions of *S. pinniger* and *S. serranoides* (Singer 1982). This was also reflected in greater stomach fullness of most species in the afternoon and early evening, indicating diurnal feeding patterns (Singer 1982). Plankton abundances were high during both day and night. However, more species were found in the water column at night. Thus, while some of these fish could do well feeding at night, daytime abundances of food seemed sufficient for their needs. Juveniles were indeed found to be most active and to feed most frequently during daylight hours, but intraspecific variability was high (Singer 1982).

Digestion was fairly slow in all species, taking at least 9 to 12 h for a full stomach of food to be half digested (Singer 1982). Together, these indicate that individuals may not need to feed every day and that both within and among species these populations may feed with a high degree of asynchrony (Singer 1982).

Do the observed differences in diets suggest interspecific competition? Central to competition theory is the presumption that individuals or populations use the same or a very similar resource and that this resource is in short supply (Pielou 1975; Pianka 1978). Abundances of all types of plankton used by these fishes are high. The fact that individuals can probably fill their stomachs in a very short time period (Singer 1982) indicates that their needs are easily met. This suggests that competition for food does not play an important role in the foraging patterns of these species. Other factors, such as the lack of observed aggressive interactions within or among the species studied in over 1,100 min of in situ feeding observations, high overlap in time of feeding, generally low similarity of diet, and high intraspecific variability within foraging patterns suggest there is little food competition (Singer 1982).

Similarly, available evidence suggests little competition for space among juveniles (Carr 1983). When juveniles enter the kelp forest system, they immediately occupy habitats characteristic of adults; thus, habitat preference may be under some genetic control. Close spatial co-occurrence with the absence of agonistic interactions suggests that competition for space is minimal in these fish. Also, within the kelp forest studied, juvenile rockfishes are the predominant planktivores, and are thus relatively free of other possible competitors. Other kelp forest planktivores such as *Chromis punctipinnis*, *Oxyjulius californica*, and *Brachyistius frenata* are present, but in very low numbers, and often only for short periods of time.

Thus, the differences in diet seen in this study appear to be the consequences of these species exploiting localized food resources encountered in different microhabitats. Competition for food does not seem to be a strong ecological influence among these juveniles.

ACKNOWLEDGMENTS

I thank Greg Cailliet, Milton Love, and Ralph Larson for their guidance and suggestions throughout this study. Many friends at Moss Landing assisted me throughout this project including Gilbert Van Dykhuizen, Bruce Welden, John Heine, Tim Herrlinger, and John Oliver, who gave helpful comments. Mark Carr and Todd Anderson gave much needed help and support in diving, stimulating comments, and general assistance. Mark Silberstein and Peter Slattery helped with invertebrate identification. Statistical services were provided by Moss Landing Marine Laboratories' HP9825 computers. The Pebble Beach Corporation graciously allowed diving access to Stillwater Cove. Partial funding for equipment came from the D & L Packard Foundation. Thanks also to Sara Warschaw and Waheedah Muhammad for typing this manuscript.

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RADIO TRACKING THE MOVEMENTS AND ACTIVITIES OF HARBOR PORPOISES, *PHOCOENA PHOCOENA* (L.), IN THE BAY OF FUNDY, CANADA

ANDREW J. READ AND DAVID E. GASKIN[1]

ABSTRACT

Eight harbor porpoises were radio-tagged (172-173 MHz) and released in the western Bay of Fundy between August 1981 and August 1983. The duration of contact with radio-tagged animals ranged from 0.3 to 22.4 days. One harbor porpoise was tracked for 22.4 days and utilized a home range area of 210 km^2. In all observed cases, the movement of radio-tagged porpoises coincided with the direction of tidal flow in the major channels and passages of the region. Analysis of 39.2 hours of ventilation sequences revealed that radio-tagged porpoises were relatively inactive from midnight until 0600 and more active during other periods.

This report documents the results of a study on the movements and activities of radio-tagged harbor porpoises, *Phocoena phocoena*, in the Bay of Fundy, Canada. The primary objective of this research was to determine the home ranges of individual harbor porpoises during the summer months. The study also provided insights into the behavior and activities of radio-tagged animals.

Studies of cetacean home ranges often rely on resightings of tagged or naturally marked animals (Irvine et al. 1981; Bigg 1982; Dorsey 1983). These methods are of limited value if individual animals travel outside the area under observation and may result in underestimation of the utilized range. A more effective means of estimating home range area is to monitor the movements of radio-tagged individuals (McDonald et al. 1979). Several recent studies have successfully employed radio-tracking techniques in field studies of cetacean species (see review by Leatherwood and Evans 1979). Notable among these are investigations of *Delphinus delphis* by Evans (1971), of *Tursiops truncatus* by Irvine et al. (1981), and of *Lagenorhynchus obscurus* by Würsig (1982).

In a preliminary study of harbor porpoise movements (Gaskin et al. 1975), we demonstrated that radio-tracking techniques could be successfully applied to this species. Although this initial research was promising, we felt that the transmitters available at that time were too large to be carried by these small porpoises (see Watson and Gaskin 1983). The recent development of smaller transmitters and the continuing availability of live porpoises from herring weirs (Smith et al. 1983) have enabled us to undertake the present study.

METHODS

The study area encompases Passamaquoddy Bay, the channels and passages around Deer Island, and waters further offshore to Grand Manan Island (Fig. 1). During the summer, mean monthly water temperatures for the upper 25 m of the water column range from 6.4° in June to 11.0°C in September (Bailey et al. 1954). The oceanography of the region is dominated by large semidiurnal tides, which have a mean amplitude of 5.5 m at North Head, Grand Manan (Anonymous 1982). The large tides generate strong currents, with velocities reaching a maximum of 2.4 m/s in Letite Passage (Forrester 1960). Further information regarding the oceanography of the region may be found in Smith et al. (1984).

Harbor porpoises were seined from herring weirs (Smith et al. 1983), placed on a sheet of open cell foam, sexed, and measured. The porpoises were liberally sprinkled with seawater throughout the tagging procedure to prevent overheating. Two 0.64 cm diameter holes were bored through the dorsal fin with a laboratory cork borer, cleansed in alcohol prior to use. The holes were immediately cold-cauterized with a histological freezing spray.

Transmitters were attached to the dorsal fin with two 0.64 cm diameter stainless steel bolts, each covered with a thin sleeve of teflon (see Figure 2). A thin, neoprene-lined plastic plate was placed between the transmitter and dorsal fin and an identical plate was positioned on the opposite side of the

[1]Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1 Canada.

Manuscript accepted November 1984.
FISHERY BULLETIN: VOL. 83, No. 4, 1985.

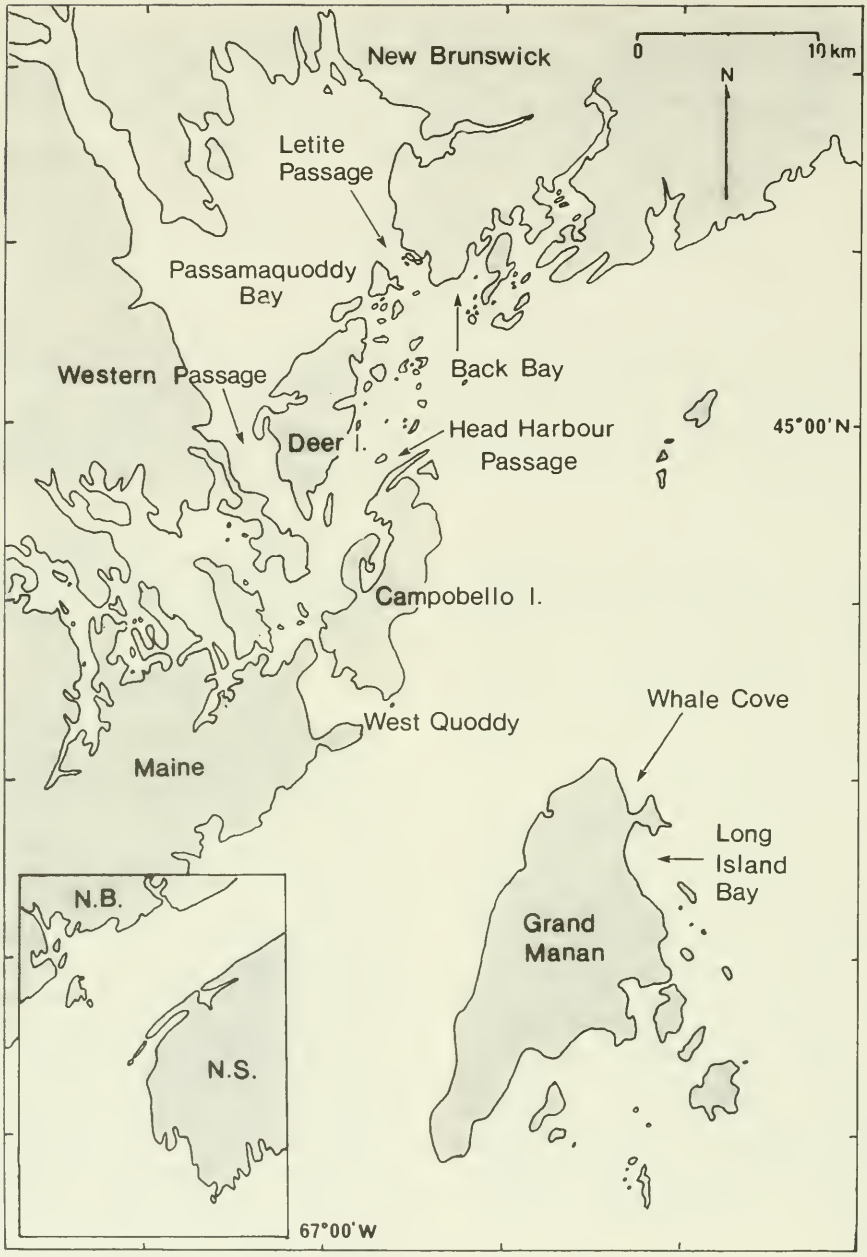


FIGURE 1.—The harbor porpoise study area with place names mentioned in text. The inset shows the study area in relation to the rest of the Bay of Fundy.

fin. The teflon-covered bolts, passed through the transmitter and plastic plates, were fastened with corrodable, low grade steel nuts.

The radio transmitters measured 3.2 × 3.8 × 6.0 cm and weighed about 170 g in air (Model 4-A, Telonics,[2] Mesa, AZ). The transmitting antennae consisted of 43 cm semiflexible whips, designed specifically for use with marine mammals.

Transmitted VHF signals (172-173 MHz) consisted

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

of 20-60 ms pulses at intervals of 0.4 s. Lithium batteries provided a maximum power output of 0.75 mW and an expected transmitting life of 1.6-6.0 mo. The maximum transmitting range across open water was about 15-20 km.

We used a Telonics TR-2 telemetry receiver with a two-element, hand-held directional antenna. The approximate direction of the transmitter was determined by rotating the antenna and noting the strongest signal. A digital data processor (Telonics TDP-2) provided a visual display of signal strength.

The position of a tagged porpoise was determined either by tracking the animal until visual contact was established, or by triangulation from shore. In the latter method, the receiving system was moved along the shore, and signal bearings at two or more locations were noted. The intersection point of these bearings was then used to approximate the position

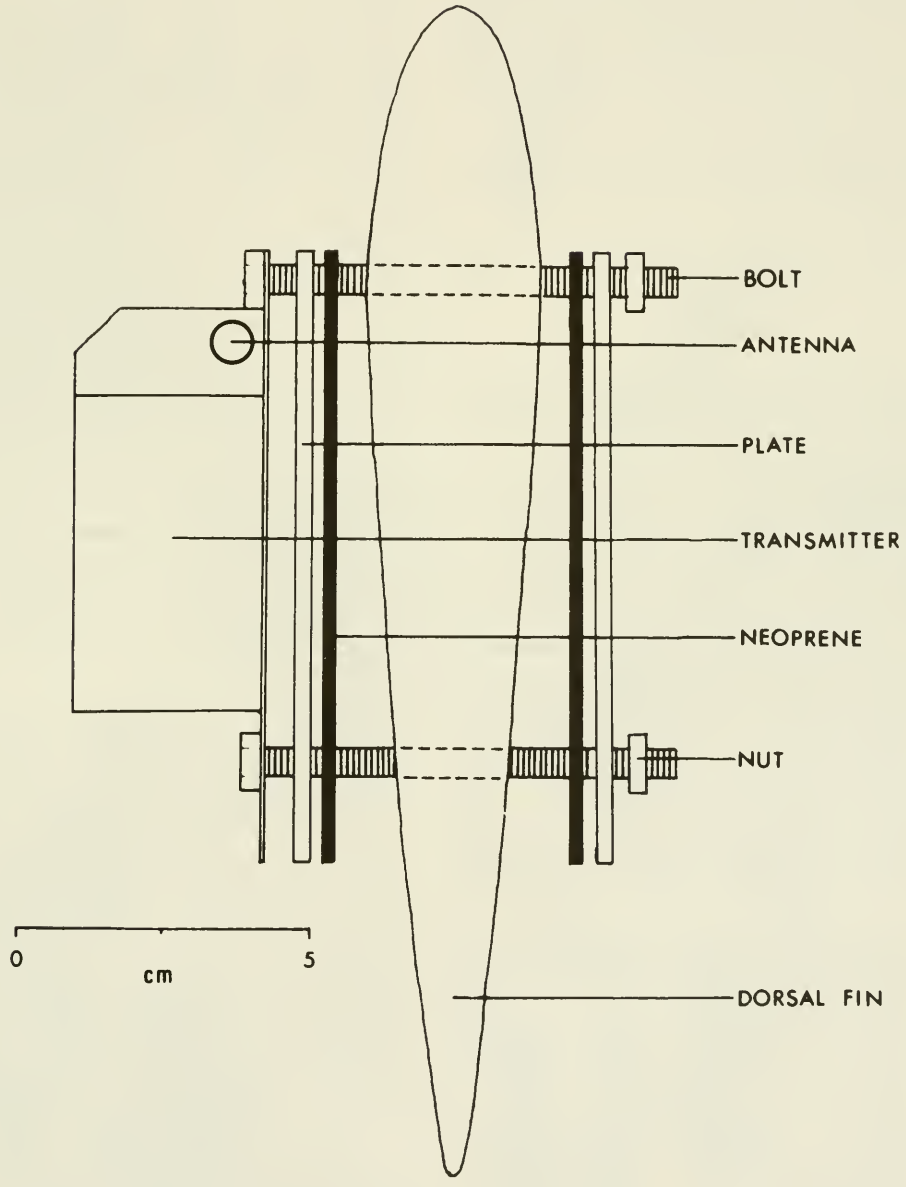


FIGURE 2.—The transmitter package used in radio-tracking studies of harbor porpoises in the Bay of Fundy. The bolts attaching the transmitter to the dorsal fin were covered by thin teflon sleeves.

of the porpoise. To ensure bearing accuracy, a series of readings were taken at each location, and the average used in triangulation (Springer 1979). Each sighting or radio location was assigned to a 1 km grid square of the Universal Transverse Mercator System. Derived radio locations were discarded if the triangulation could not place a porpoise within a 1 km square; the time elapsed between fixes and bearing error ($\pm 5°$) precluded more precise estimation. Positional data were collected at least once a day, but usually on a more frequent basis.

The radio signal was received only when the transmitting antenna was exposed, allowing the duration of both submergence and surface periods to be recorded. Such ventilation data were collected on an opportunistic basis throughout the tracking period of each porpoise.

A detailed analysis of the methods used in this study is presented in Read and Gaskin (1983).

RESULTS

Movements

Eight harbor porpoises were released carrying transmitters over the course of the study (Table 1). During the attachment procedure, porpoises were out of the water for a mean of 6.6 min (SD $\pm$ 1.4, n = 8), during which time most animals remained fairly still. Only two porpoises exhibited any trauma while being handled; RT-5 vomited briefly, and RT-7 (a 110 cm calf) repeatedly lashed its flukes. The latter porpoise appeared momentarily disoriented when returned to the water, but quickly resumed swimming and surfacing normally after being joined by a larger porpoise. The larger animal, presumably the calf's mother, had also been trapped in the weir, but escaped overnight and remained in the vicinity until the calf's release.

Duration of radio contact ranged from 0.30 (RT-5) to 22.4 d (RT-2), with a mean of 5.1 d (SD $\pm$ 7.1, n = 8). In some instances, loss of radio contact may have been due to the premature release of the transmitter package. The rear bolt attaching the transmitter to the dorsal fin of RT-3 was missing when the porpoise was photographed 5 h before signal loss occurred. The radio signals of RT-3 and RT-7 were being monitored when contact was lost, and in both cases termination of the signal was abrupt, a pattern compatible with the hypothesis of transmitter loss. In our limited observations of radio-tagged porpoises (see below), we did not see any evidence of displacement of the transmitter package (Irvine et al. 1982).

Over the course of the study, three porpoises were released from the same weir in Whale Cove, Grand Manan. Attempts to relocate RT-1, the first porpoise released in Whale Cove, were frustrated by fog and heavy seas which persisted for the entire 3-d tracking period. In addition, the shoreline configuration of northern Grand Manan prevented accurate triangulation. However, the strength and direction of the signal received from shore indicated that the porpoise remained in the vicinity of northern Grand Manan until signal loss occurred. The movements of the other two porpoises released in Whale Cove (RT-3 and RT-7) are illustrated in Figure 3A and B.

On 30 August 1982, four porpoises were reported trapped in a weir in Back Bay, mainland New Brunswick. A female (RT-4), accompanied by a 101 cm calf, and a young male (RT-5) were released on 31 August. The remaining porpoise, another young male (RT-6), was tagged and released the following day. RT-4 and RT-5 remained together for at least 7 h, after which contact was lost with RT-5. The movements of RT-4 and RT-6 are depicted in Figure 3C and D.

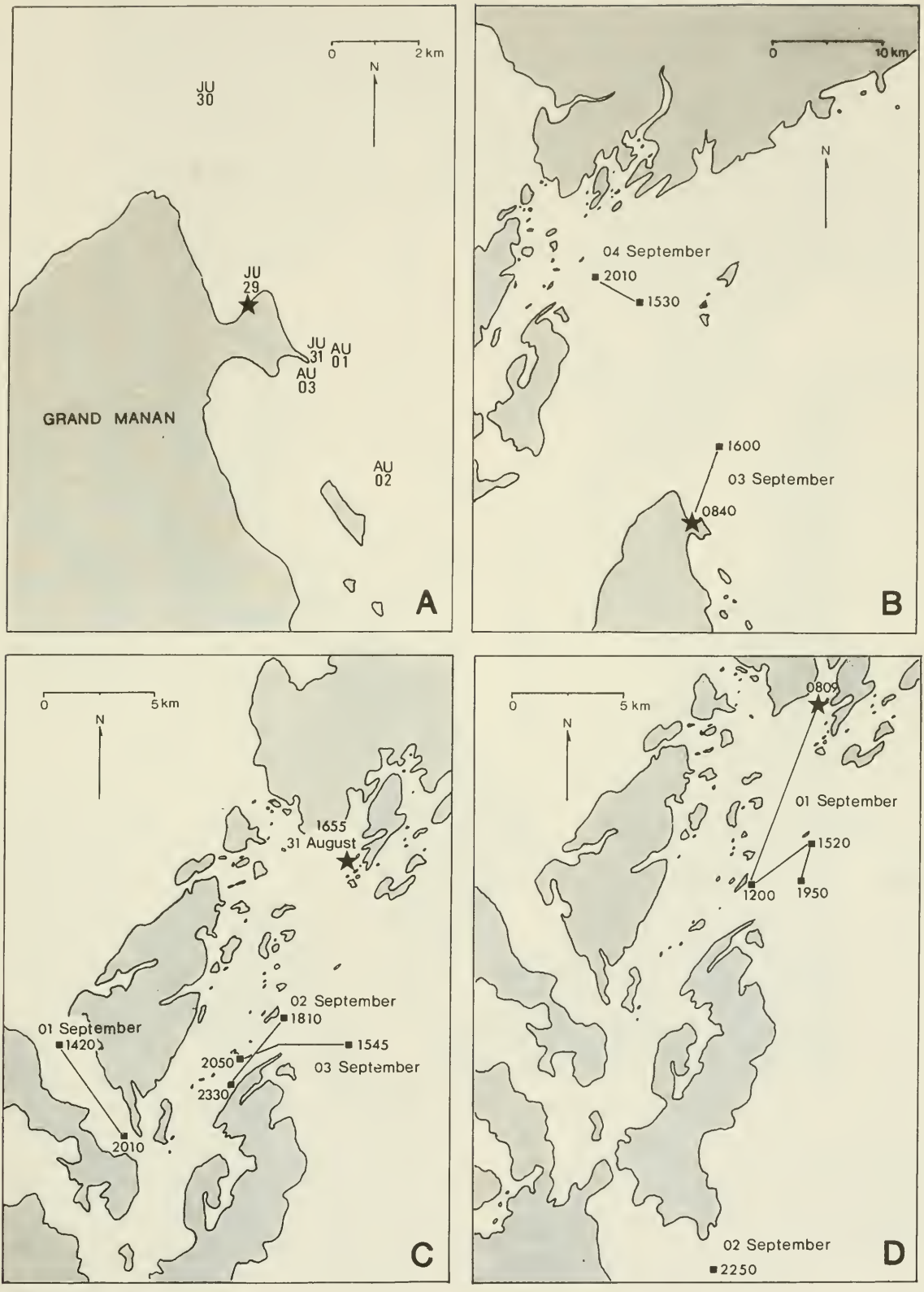
The longest tracking sequence recorded in this study was that of RT-2, released near St. Andrews, mainland New Brunswick. This porpoise spent the majority of its 22-d tracking period within Passamaquoddy Bay, although occasional excursions were made to the east of Deer Island (Fig. 4). The home range of RT-2, calculated using the convex polygon method, was about 210 km^2 (excluding land masses).

RT-8, the only porpoise to be radio-tagged in 1983, travelled from its release point in northern Passamaquoddy Bay to West Quoddy in about 48 h. Logistical constraints prevented more precise determination of the movements of this animal.

TABLE 1.—Data summary for harbor porpoises radio-tagged and released in the western Bay of Fundy.

Porpoise code	Length (cm)	Sex	Frequency (MHz)	Date of Release	Duration of contact (d)
RT-1	132	M	173.350	05 08 81	3.05
RT-2	119	M	173.550	20 08 81	22.4
RT-3	145	M	173.500	29 07 82	5.32
RT-4	131	F	173.100	31 08 82	3.16
RT-5	114	M	173.000	31 08 82	0.30
RT-6	116	M	173.700	01 09 82	2.72
RT-7	110	M	173.650	03 09 82	1.83
RT-8	114	M	172.600	09 08 83	2.25

FIGURE 3.—Movements and positions of radio-tagged harbor porpoises in the Bay of Fundy. The release point of each porpoise is indicated by a star. A) Position of porpoise RT-3 at 1200 of each day of tracking period; B) Movements of porpoise RT-7; C) Movements of porpoise RT-4; D) Movements of porpoise RT-6.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30
JU
29
JU
31
AU
01
AU
03
GRAND MANAN
AU
02
A
0
10 km
N
04 September
2010
1530
1600
03 September
0840
B
0
5 km
N
1655
31 August
02 September
1810
01 September
1420
1545
2050
03 September
2330
2010
C
0
5 km
N
0809
01 September
1520
1200
1950
02 September
2250
D

FIGURE 4.—Position of porpoise RT-2 at 1200 of each day of tracking period in the western Bay of Fundy.

The movements of three radio-tagged porpoises (RT-2, RT-4, RT-6) were tracked through the major passages around Deer Island on seven occasions. In all cases, the direction of movement coincided with the direction of tidal flow. The strong correlation between porpoise movements and current direction in these areas was demonstrated on 30 August 1981, when RT-2 moved up Western Passage with the flood tide, turned at slack high water and moved out with the ebb.

Two radio-tagged porpoises were resighted on several occasions. RT-2 was observed resting at the surface in the approaches to Head Harbour Passage on 22 August 1981. Although the porpoise was alone, several groups of resting animals were present in the vicinity. RT-3 was resighted on six occasions; during five of these sightings the radio-tagged animal was accompanied by a single large porpoise. These observations gave no indication that the transmitter packages affected the behavior of tagged porpoises.

Attempts to relocate radio-tagged animals demonstrated some of the inherent problems involved in censusing harbor porpoise populations. Even with the aid of directional receivers and brightly painted transmitters, it was difficult to sight a tagged porpoise or to follow its movements after it had been located. It proved particularly difficult to see radio-tagged porpoises while they lay motionless at the surface.

Patterns of Activity

In total, 39.2 h of ventilation sequences were recorded from four radio-tagged porpoises (RT-2, RT-3, RT-4, RT-7). These sequences comprised 4,680 individual dives, lasting from 2 to 195 s.

Two types of signals were received from radio-tagged animals. The most common signal was brief (1-3 s) and indicated that the porpoise had surfaced and submerged in a continuous motion. Such action patterns are commonly referred to as rolls (Amundin 1974; Smith et al. 1976). Other signals were more prolonged (4-100 s) and are referred to here as surface periods.

Prolonged signals received from radio-tagged harbor porpoises have previously been interpreted as near-surface swimming (Gaskin et al. 1975). However, visual observations of radio-tagged animals RT-2 and RT-3 indicated that such signals originated from porpoises resting motionless at the surface. The strength of the transmitted signal attenuated rapidly as the length of exposed antenna decreased, making it unlikely that signals could be received at any distance from porpoises swimming just below the surface (see also Frost et al.[3]).

Radio-tagged porpoises exhibited two readily discernible activity states (Fig. 5). Low activity (or relative inactivity) was characterized by frequent surface resting periods interspersed with rolls; resting periods accounted for over 55% of all signals in this activity state. Porpoises were considered active (high activity) when resting periods were absent or infrequently recorded. It is important to note that porpoises did not rest at the surface when wave height was >30 cm and winds speeds exceeded 13 km/h (see also Dudok van Heel 1962; Andersen and Dziedzic 1964).

[3]Frost, K. J., L. F. Lowry, and R. R. Nelson. 1983. Investigations of belukha whales in coastal waters of western and northern Alaska, 1982-1983; marking and tracking of whales in Bristol Bay. Final Report, Contract NA 81 RAC 00049, 104 p.

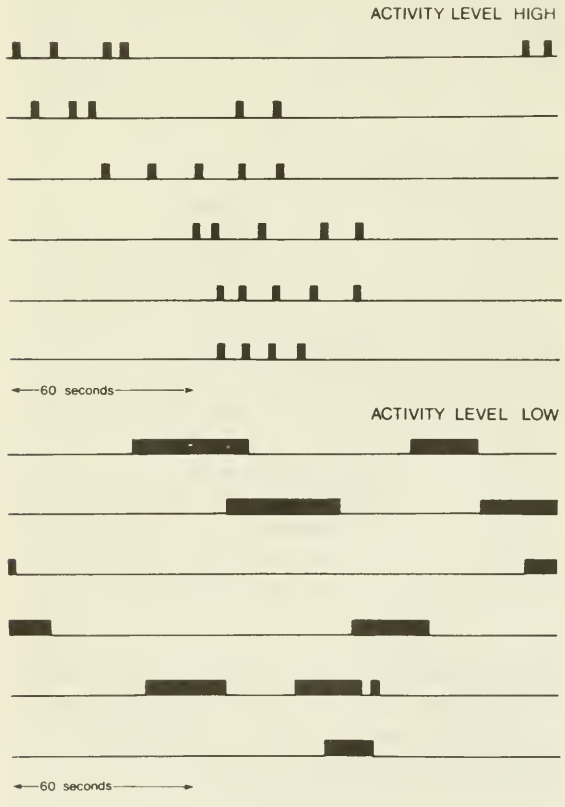

FIGURE 5.—Examples of signal patterns used to derive activity states of radio-tagged harbor porpoises (each example represents a continuous record). Activity level was considered high when signals were dominated by rolls (signal duration 1-3 s). Activity level was considered low when signals were dominated by surface resting intervals (signal duration >3 s). The signal pattern used to demonstrate the high activity level (top) is characteristic of Pattern B respiration (Watson and Gaskin 1983).

Radio-tagged porpoises exhibiting the high activity state expressed two ventilation patterns; these are described using the terminology of Watson and Gaskin (1983). Most data recorded in this activity state consisted of Pattern B, a series of long dives, each followed by a sequence of several rolls (see Figure 5). Less commonly observed was Pattern A, in which single rolls followed relatively short submergences (seldom exceeding 30 s in duration). Pattern A was exhibited for brief periods only (5-16 min) and comprised <4% of all signals recorded during high activity sequences.

Ventilation data recorded from RT-2 and RT-4 were dominated by low activity sequences. However, low activity sequences were not recorded from either RT-3 or RT-7. Although RT-3 was frequently observed resting at the surface, the loose transmitter package (see above) caused the antenna to reflect backwards, allowing signal reception only during rolls. Thus, it was not possible to accurately monitor the duration of resting periods for this porpoise. Data from RT-7 were acquired only during periods of high winds and heavy seas which precluded surface resting behavior.

Because surface resting was the criterion on which determinations of activity levels were based, it was impossible to ascertain the activity level of radio-tagged porpoises in periods of high winds and heavy seas. To construct an activity budget, therefore, it was necessary to exclude data recorded during periods when surface resting was not possible. A total of 10.5 h of ventilation sequences were recorded under such conditions. In addition, data acquired from RT-3 were excluded because of the bias imposed by the transmitting system. After these data had been deleted, 24.5 h of ventilation sequences recorded from RT-2 and RT-4 remained.

Both RT-2 and RT-4 were relatively inactive from midnight until 0600, spending over 90% of this period in the low activity state. Both porpoises spent a considerable portion of this time resting at the surface (Table 2). During this period of reduced activity, the porpoises were seldom located in nearshore areas, although they frequented such areas during other periods. The two porpoises were highly active for 35% (RT-2) and 36% (RT-4) of daylight and evening hours (0600 until midnight) (Table 2).

DISCUSSION

Movements and Ranges

Radio-tagged harbor porpoises demonstrated considerable mobility within the study area, often moving distances of 15-20 km in a 24-h period. These results are similar to those previously reported from radio-tagged harbor porpoises in the region (Gaskin et al. 1975). Other inshore odontocete species exhibit daily movements of a similar magnitude. For example, dusky dolphins, *Lagenorhynchus obscurus*, tracked by Würsig (1982), travelled a "mean minimum distance" of 19.2 km each day. However, pelagic species apparently travel over much greater distances. A pelagic spotted dolphin, *Stenella attenuata*, tracked by Leatherwood and Ljungblad (1979), travelled over 100 km in a 12-h period, while common dolphins, *Delphinus delphis*, may cover distances of 70-140 km each day (Evans 1971).

The mobility exhibited by the majority of radio-tagged porpoises suggest that the ranges of these animals were similar to that calculated for RT-2 (210 km^2). Only one other study has examined the areas of home ranges utilized by odontocete cetaceans. Wells et al. (1980) used resightings of naturally marked animals to estimate the size of bottlenose dolphin, *Tursiops truncatus*, ranges in the coastal waters of western Florida. The mean home ranges of these dolphins varied with age and sex, and ranged from 15 to 41 km^2. It is possible that the apparent difference in the size of home ranges of these two species reflects the exploitation of different prey species. In the Bay of Fundy, harbor porpoises feed predominantly on juvenile herring, *Clupea harengus* (Smith and Gaskin 1974), which exhibit a high degree of mobility (Jovellanos and Gaskin 1983). In contrast, Florida bottlenose dolphins are opportunistic predators on species such as mullet *Mugil cephalus*, which may be more sedentary in nature (Irvine et al. 1981).

Patterns of Activity

The patterns of activity observed in the present

TABLE 2.—Activity patterns of radio-tagged harbor porpoises RT-2 and RT-4 in the western Bay of Fundy. The low activity state was characterized by frequent surface resting periods, which were infrequent or absent in the high activity state. Only data recorded during calm conditions have been included.

Porpoise	Time	Observation time (min)	Activity: high (%)	Activity: low (%)	At surface (%)
RT-2	0000-0559	352.9	2.0	98.0	31.4
	0600-1159	274.8	14.9	85.1	18.8
	1200-1759	435.2	46.0	54.0	11.2
	1800-2359	165.2	41.0	59.0	12.2
Total		1,228.5	25.7	74.3	18.8
RT-4	0000-0559	116.0	7.0	93.0	18.5
	0600-1159	37.0	100.0	0.0	0.0
	1200-1759	0.0	—	—	—
	1800-2359	90.7	9.9	90.1	13.6
Total		243.7	22.2	77.8	13.9

study do not support previous contentions that the metabolic requirements of harbor porpoises (see Kanwisher and Sundnes 1965) are such that individuals must spend a large proportion of each day engaged in foraging behavior (Smith and Gaskin 1974; Watson and Gaskin 1983).

Herbers (1981) has hypothesized that behavioral inactivity is a product of predation efficiency. As predation efficiency increases, less time is spent searching for and capturing prey, and more time is available for other behavior, including inactivity. Therefore, if harbor porpoises are efficient predators, it seems reasonable to suggest that only a small portion of their day would be spent engaged in foraging behavior.

Many other mammalian predators are inactive for large portions of the day. For example, Serengeti lions, *Panthera leo*, are inactive for about 85% of each day (Schaller 1972). Similarly, spotted hyaenas, *Crocuta crocuta*, are inactive for 84% of the day (Kruuk 1972). Even the sea otter, *Enhydra lutris*, with a metabolic rate 2.4 times that predicted for a terrestrial mammal of equal size (Costa and Kooyman 1982), spends only 34% of each day foraging (Loughlin 1979).

The ventilation sequences recorded from RT-2 and RT-4 suggest that these harbor porpoises restricted the majority of their activity to daylight and evening hours (Table 2). If a circadian pattern of activity exists, it may be related to the schooling behavior of prey species. The structure of herring schools breaks down after dusk, as the visual cues used to maintain school structure become inoperative (Brawn 1960). Thus, the fish exhibit a dispersed distribution at night, presumably limiting prey capture by predators such as the harbor porpoises, which rely on dense schools to maintain maximum capture efficiency.

Other odontocete species exhibit various circadian patterns of activity. Observations of captive bottlenose dolphins indicate that, like the harbor porpoise, *Tursiops* is relatively inactive at night (McBride and Hebb 1948; McCormick 1969; Saayman et al. 1973). In contrast, Hawaiian spinner dolphins, *Stenella longirostris*, rest during the day and feed almost exclusively at night (Norris and Dohl 1980). The prey of spinner dolphins undertake extensive vertical migrations (Perrin et al. 1973) and may be more available to the dolphins at night.

We were interested in observing the nocturnal behavior of harbor porpoises (when they were presumably relatively inactive) under conditions of strong winds and heavy seas, when surface resting was not possible. Ventilation data recorded from RT-7 during a 5-h period (0000-0500, 5 September 1982) of heavy seas consisted almost exclusively of Pattern B sequences. Watson and Gaskin (1983) have suggested that this ventilation pattern is expressed primarily by foraging porpoises, but it seems unlikely that RT-7 (a calf) was foraging for 5 consecutive hours at night. An alternative explanation is that the porpoise was resting underwater and rising to the surface for a series of breaths (see similar observations by McBride and Hebb 1948; Layne 1958; McCormick 1969; Condy et al. 1978). It is possible, therefore, that harbor porpoises engaged in diverse behavioral activities may exhibit similar ventilation patterns.

During the period of reduced activity (from 0000 to 0600) radio-tagged porpoises were often located in open water some distance from shore. This may reflect a tendency for porpoises to rest in areas where the hazards of swift currents and shallow waters are minimized. Observations made in the inshore waters of the Deer Island region confirm that porpoises seldom rest at the surface in nearshore environments (Watson and Gaskin 1983).

ACKNOWLEDGMENTS

We thank W. Kozak and the members of the Fundy Weir Fishermen Association for their assistance in this study. Sterling field assistance was provided by C. Thomson and members of the Fundy Cetacean and Seabird Research Group. Constructive criticism of earlier versions of this paper were provided by B. Braune, L. Murison, P. Watts, L. White, and two anonymous reviewers. This research was supported by Joint Contract UP-G-152 (Departments of Supply and Services and Fisheries and Ocean Canada). Harbor porpoises were tagged under a permit issued by Fisheries and Oceans Canada.

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EARLY POSTNATAL GROWTH OF THE SPOTTED DOLPHIN, *STENELLA ATTENUATA*, IN THE OFFSORE EASTERN TROPICAL PACIFIC

ALETA A. HOHN[1] AND P. S. HAMMOND[2]

ABSTRACT

Estimates of length at birth and early postnatal growth are made for the northern and southern populations of the offshore spotted dolphin in the offshore eastern tropical Pacific. Length at birth is estimated to be 85.4 cm for the northern population and 83.2 cm for the southern population. Analyses of series of monthly distributions of length revealed two cohorts born each year in the northern population, at least in the northern inshore part of its geographic range, but only one cohort born each year in the southern population. Growth curves fitted to the means of the monthly distributions of length gave estimates of length at 1 year of 126.2 and 132.6 cm and length at 2 years of 154.3 and 154.9 cm for the two cohorts in the northern population, and length at 1 year of 127.9 cm for the southern population. A growth curve fitted to lengths and ages (in dental growth layer groups) from the northern population gave estimates of lengths at 1 and 2 years of 123.0 and 143.0 cm, respectively.

The average growth rate of individual animals in a population is an important characteristic because of its correlation with other population parameters. In fisheries biology, two commonly employed techniques used to estimate growth rates are the aging of a sample of fish of known length and the following of a series of length distributions through time. These techniques allow the relationship between length and age (or relative age) to be applied to a much larger sample of fish, provided that the aged sample is a representative one.

For most species of fish, length-age relationships may be appropriate for the entire life of the animals, or at least for the period of interest to a commercial fishery. In marine mammals, however, length changes little, if at all, after attainment of physical maturity. Growth rates may change markedly even while the animal is maturing, being high for an initial period after birth and then declining quite rapidly. In delphinids, the growth rate has been found to be high in the first year, with animals typically increasing by 50-70% of their birth length (Sergeant 1962; Kasuya et al. 1974; Kasuya 1976; Miyazaki 1977; Hohn 1980; Perrin and Henderson 1984), but then declined rapidly in the second year. During this period, growth rates are high relative to the variability in age-at-length so that length distributions are distinguishable as separate age groups. Consequently, length-age relationships for these animals are most useful from birth until about 2 yr.

In this paper, we have used both the technique of following a series of length distributions from month to month and the technique of aging a sample of dolphins of known length to estimate the rate of growth in the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific (hereafter referred to as the offshore spotted dolphin). In neither of these two techniques did we have an absolute measure of age. Consequently, we have estimated length at birth independently and used this to fix time at birth. Growth curves were fitted to the length data by relative age and then length at birth was substituted in order to predict length-at-age.

THE SAMPLE

The field data and specimens used in the following analyses were collected by National Marine Fisheries Service (NMFS) and Inter-American Tropical Tuna Commission (IATTC) scientific technicians aboard commercial tuna purse seiners from 1968 to 1982. Procedures for collecting sample data and specimens have been described by Perrin et al. (1976). In all the following analyses, the data have been stratified into northern and southern popula-

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.
[2]Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, La Jolla, CA 92098; present address: Sea Mammal Research Unit, c/o British Antartic Survey, Madingley Road, Cambridge CB3 OET, United Kingdom.

Manuscript accepted December 1984.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

tions divided by lat. 1°S, based on a division selected by Perrin et al. (1979). Areas 1 and 2 in Figure 1 correspond to the region occupied by the southern offshore spotted dolphin and areas 3-8 correspond to the region occupied by the northern offshore spotted dolphin.

ESTIMATION OF LENGTH AT BIRTH

An accurate estimate of length at birth is important because it establishes a point through which any growth curve should pass. This extra degree of freedom allows greater accuracy in fitting growth curves and estimating growth rates. Neither of our methods of relating length to age, described below, allows us to fix absolute age so it is essential here for us to calculate an independent estimate of length at birth.

A commonly used method of estimating length at birth when a sufficient sample is available is to regress the percent postnatal at each length interval on length and to calculate the length at which 50% of the specimens are predicted to be postnatal. This method, using a linear model, has been employed to estimate length at birth for spotted dolphins (Perrin et al. 1976), for striped dolphins, *S. coeruleoalba*, (Miyazaki 1977), and for spinner dolphins, *S. longirostris*, (Perrin et al. 1977), and using a nonlinear model for spinner dolphins (Perrin and Henderson 1984). Another method commonly employed when a small sample is available is to estimate the average length at birth as the mean length of known neonates or the mean length of full-term fetuses and small calves combined. This method has been used to estimate length at birth for long-finned pilot whales (Sergeant 1962), for spotted dolphins (Kasuya et al. 1974), for bottlenose dolphins, *Tursiops truncatus*, (Ross 1977; Hohn 1980), and for

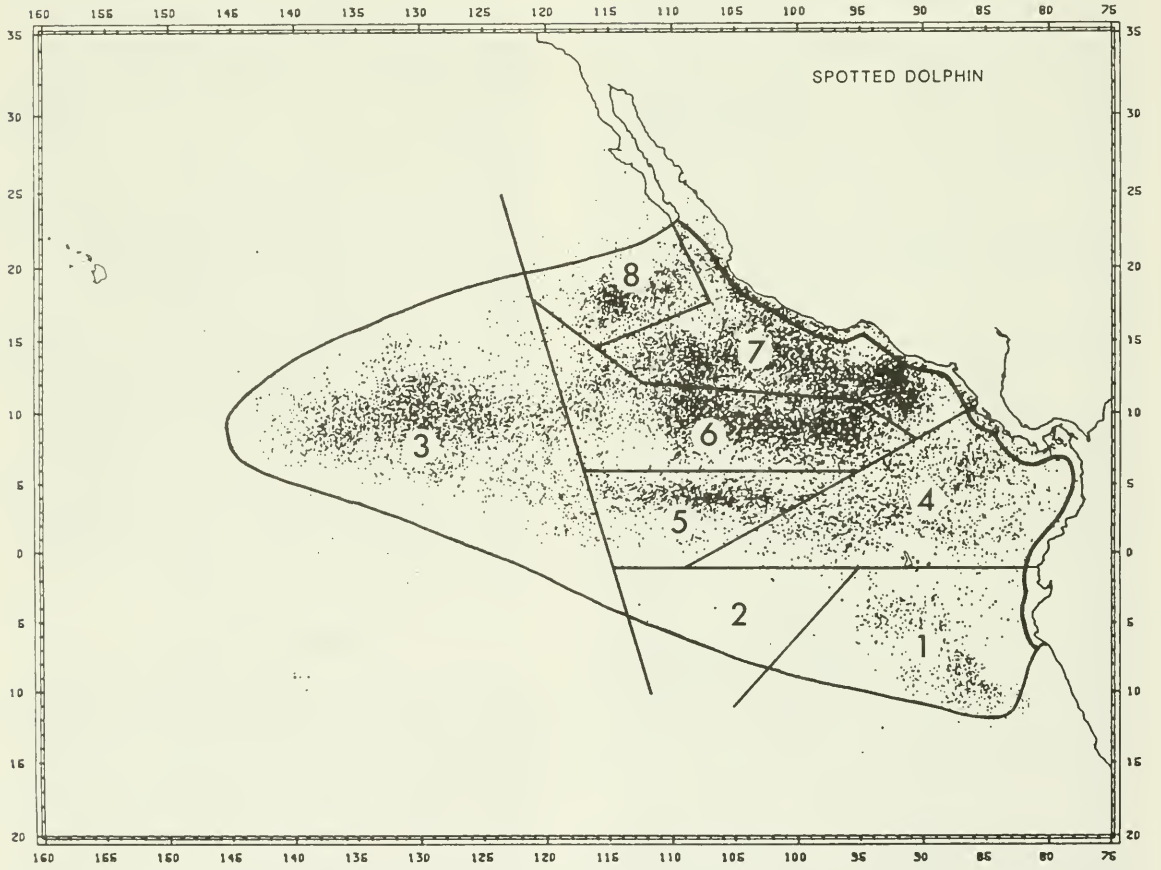

FIGURE 1.—Areas inhabited by the offshore spotted dolphin. The numbered regions refer to strata investigated in analyses of monthly distributions of length. In all analyses, the southern population is from areas 1 and 2, and the northern population is from areas 3 through 8.

the franciscana dolphin, *Pontoporia blainvillei*, (Kasuya and Brownell 1979).

Methods

The data used in this analysis were from all fetuses and calves sampled between 1973 and 1981 except for three specimens <68 cm identified as calves and one specimen of 91 cm identified as a fetus (n = 609). These four specimens were judged to have been misidentified. The data were stratified by area, north and south of lat. 1°S, and the northern sample was further stratified by the size of kill in each net set. Powers and Barlow (1979[3]) have shown that in net sets in which the kill of spotted dolphins from the northern offshore regions was ⩽40 (small-kill sets), about twice as many calves were killed as a proportion of the total kill as in sets where the kill was >40 (large-kill sets). This would introduce a bias in the estimate of length at birth in the regression procedure because about 90% of all northern specimens were from small-kill sets. The effect would be to underestimate length at birth because the ratio of calves to fetuses was too high in most of the sample. To investigate the extent of the bias, we calculated average length at birth for all northern specimens, for specimens from sets with kill ⩽40 and >40, and for specimens from sets with kill ⩽30 and >30 because the sample size for sets with kill >40 was small. The small sample available for southern specimens prevented any further stratification of the data.

Length at birth was estimated by fitting a logistic model to the percent postnatal at each length interval, weighted by the inverse of the binomial variance of each percentage, and estimated by calculating from the fitted curve the length at which 50% of the specimens were predicted to be postnatal. We also investigated linear and asymmetric logistic-type models.

Results

Figure 2 shows the length-frequency data for northern specimens from sets with kill ⩽40, and the logistic model fitted to the data. Figure 3 is the equivalent for northern specimens from sets with kill >40. Table 1 gives the results for all stratifications described above using the logistic model. Using the linear or asymmetric logistic-type models did not improve the fit and gave similar results.

Table 1 shows that the estimates of length at birth for northern specimens using the unstratified data (82.0 cm) and using specimens from sets with kill ⩽30 (81.6 cm) or ⩽40 (81.6 cm) are lower than the estimates using specimens from sets with kill >30 (84.6 cm) or >40 (85.4 cm), demonstrating that the bias resulting from an overrepresentation of calves in small-kill sets is significant. Furthermore, the estimate for kill >40 is higher than that for kill >30, indicated that the proportion of calves in the sample may still be a function of kill-per-set at this level. Further stratification to investigate whether or not estimates of length at birth continue to rise at higher thresholds of kill-per-set was not possible because of small sample size.

The estimate of length at birth for southern specimens is 83.2 cm. No stratification was possible because of the small sample.

Estimates of standard deviations of the estimates of length at birth are not given because, in fitting the logistic model, sums of squares were minimized for differences between observed and predicted percent postnatal and it was unclear how to calculate the standard deviations.

TABLE 1.—Estimates of length at birth stratified by number of offshore spotted dolphins killed per set. The range of length classes includes the last 0% postnatal length class and the first 100% postnatal length class.

	Sample size	Range (cm)	Length at birth predicted from the logistic model (cm)
Northern offshore spotted dolphin			
Unstratified data	586	71-92	82.0
Sets with kill ⩽30	321	73-92	81.6
Sets with kill ⩽40	384	71-92	81.6
Sets with kill >30	105	71-89	84.6
Sets with kill >40	36	78-89	85.4
Southern offshore spotted dolphin			
Unstratified data	23	78-85	83.2

Discussion

Our estimate of length at birth of 82.0 cm from the unstratified northern data is similar to that of Perrin et al. (1976), who estimated length at birth at 82.5 cm, based on a sample of 73 northern specimens (calves and fetuses) grouped into 3 cm intervals from 74 to 92 cm.

Estimates of length at birth in large-kill sets are less biased because of the overrepresentation of calves in small-kill sets. A future larger sample from large-kill sets may allow for additional stratification by kill-per-set, enabling estimates to be calculated

[3]Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, Status of Porpoise Stocks Workshop, La Jolla, CA, 27-31 August 1979. Unpubl. MS.

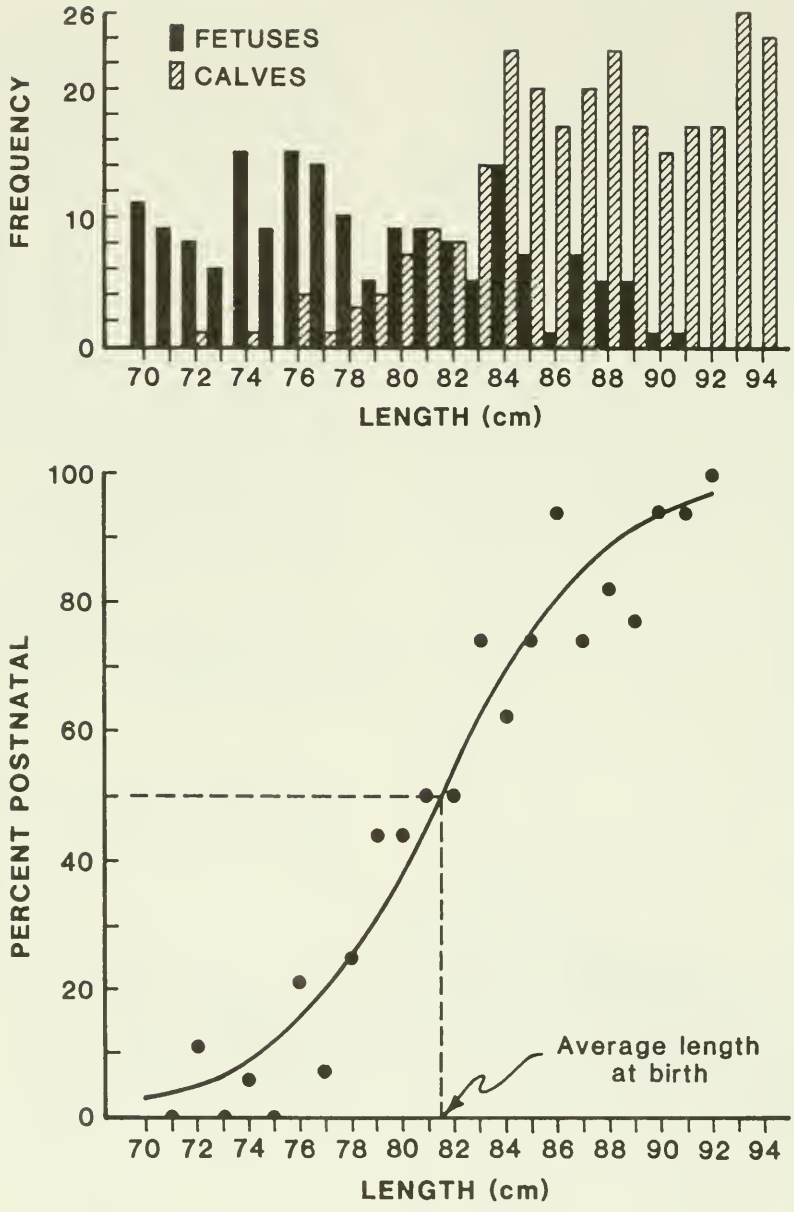

FIGURE 2.—Length-frequency data for specimens from sets with kill ≤40 grouped in 1 cm intervals for 163 fetuses and 221 calves from the northern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

using specimens from sets with higher levels of kill. It may then be possible to determine at what level of kill-per-set the estimate ceases to increase. Until additional data are available, we consider 85.4 cm to be the best estimate of length at birth in northern offshore spotted dolphins.

Our estimate of length at birth in the southern offshore spotted dolphin of 83.2 cm is more questionable because we were unable to stratify by kill-per-set. As adults, southern specimens are about 2.5 cm shorter than their northern counterparts (Perrin et al. 1979). This small, but statistically significant, difference may or may not imply that length at birth is smaller in the southern population. The small sample of 23 specimens used in our calculation of length at birth raises doubts concerning the

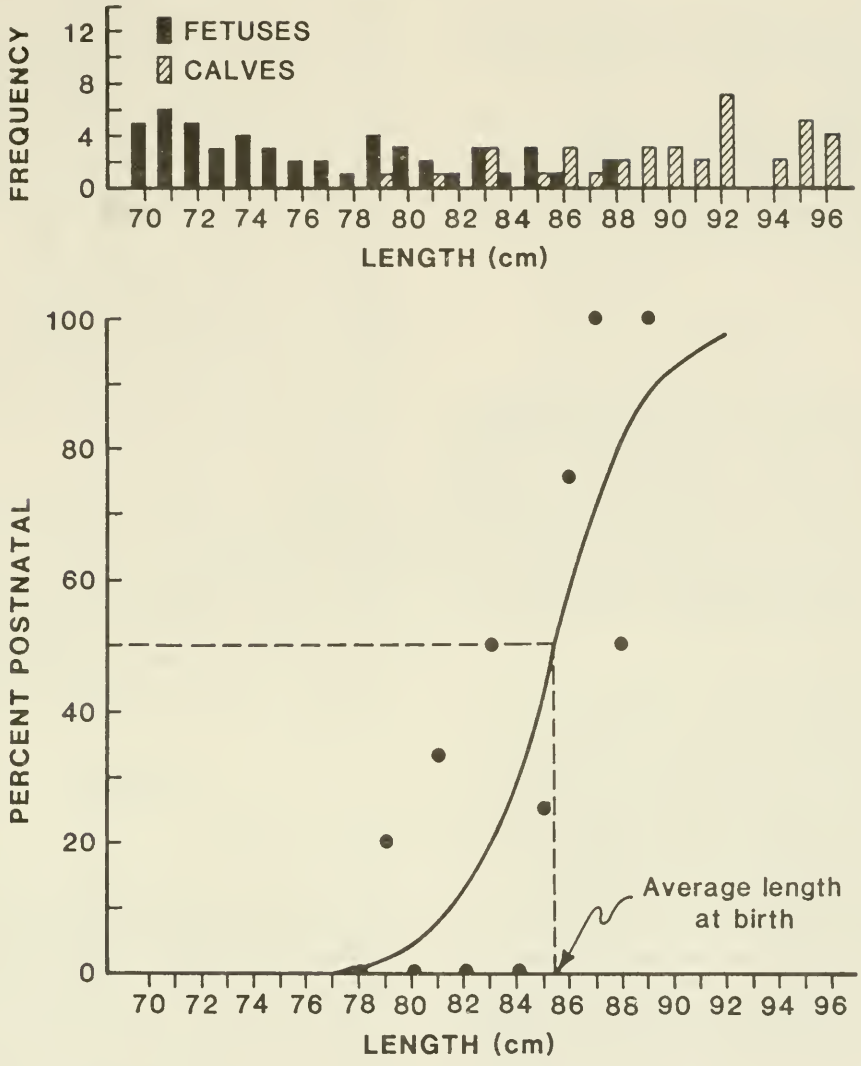

FIGURE 3.—Length-frequency data for specimens from sets with kill >40 grouped in 1 cm intervals for 21 fetuses and 15 calves from the southern offshore population of spotted dolphins, and the logistic model fitted to the percentage of animals that were postnatal.

accuracy of this estimate. For these reasons, we take the estimate from all southern specimens of 83.2 cm as our provisional best estimate of length at birth for southern offshore spotted dolphins while recognizing that this estimate may be biased downwards because of a possible overrepresentation of calves in the sample.

ESTIMATION OF LENGTH-AT-AGE USING ANALYSES OF MONTHLY DISTRIBUTIONS OF LENGTH

Perrin et al. (1976) used the technique of fitting a growth curve to the means of normal distributions fitted to length-frequency data by month to estimate the length of the offshore spotted dolphin at 1 yr of age. Perrin and Henderson (1984) used the same technique for the spinner dolphin. The technique is based on the assumption that breeding in these dolphins is seasonal and that a cohort of animals born at approximately the same time is characterized by a distribution of lengths, identifiable as a mode in the overall length distribution, which can be followed from month to month as mean length of the cohort increases. If there are sufficient data in each month, mean lengths can be followed from birth until

growth slows to an extent that distributions of lengths from different cohorts cannot be distinguished. A growth curve can then be fitted to the monthly mean lengths.

Since the analysis of Perrin et al. (1976), the sample of measured lengths from offshore spotted dolphins has increased from about 3,500 to over 15,000. Consequently, we were able to analyze the available data more extensively than had been done previously.

Methods

Length measurements from all postnatal specimens, made between 1968 and 1982, were used in the analyses except for three specimens <68 cm which were judged to have been erroneously identified as calves. The data were stratified into eight areas based upon apparent hiatuses in distribution from examination of sightings and effort data (Fig. 1). Areas 1 and 2 comprise the southern population and areas 3-8 the northern population.

For the northern data, no consistency could be found in preliminary analyses of lengths when data from all areas were included. When area 3 was excluded, consistency was much improved. When areas 4 and 5 were also excluded, consistency was improved further for the months of February through June. This indicated that there were nonseasonal or seasonal but asynchronous elements in areas 3, 4, and 5 at least at certain times of the year. Consequently, in our analyses of northern data we used lengths from areas 6, 7, and 8 only for February through June and lengths from areas 4-8 for January and July through December. A similar situation occurred for the southern data where the elimination of area 2 improved consistency for January through May. In our analyses of southern data, therefore, we used lengths only from area 1 for these months.

The data were grouped in interval widths of 4 cm. This gave four possible ways of grouping the data because lengths were measured to the nearest whole centimeter. Each of these four groupings were investigated, there being no reason to prefer a starting point of the first interval as, for example, 76, 77, 78, or 79 cm.

A mixture of normal distributions was fitted to each data set using a version of the computer program NORMSEP (Hasselblad 1966). The program requires the number of distributions to be specified, and this was varied in order to determine the most likely number of distributions present. The model selected as most representative of the length-frequency data was that which gave the highest χ^2 value, and therefore the highest probability that a greater χ^2 value could be obtained by chance alone, and also gave biologically feasible results based on prior knowledge of delphinid growth. (Some model fits had a very high probability of a greater χ^2, but the mean lengths could not be accounted for by any reasonable regime of growth.)

We chose Laird's (1969) form of the Gompertz (1825) growth equation to fit to the monthly mean lengths. A linear model is clearly inadequate to describe growth except over a very short time period. We also investigated the use of the von Bertalanffy (1934) growth equation but found it to be less flexible than the Gompertz model.

Each model of growth was fitted to the mean lengths using the midpoint of the first month as time zero. In fact, this is not necessarily the time of birth so we fixed time of birth by substituting our estimate of length at birth into the fitted equation. Lengths at age were then calculated by substituting that age plus the difference between the midpoint of the first month and our calculated time of birth into the fitted equation.

Results

Northern Population

Figure 4 shows, as examples, the fitted mixture of normal distributions to the length-frequency data for August and October. The arrows indicate the positions of the means of the fitted distributions.

Table 2 shows the estimates of mean length of the fitted normal distributions for each month. The estimates are presented so that the increases from month to month can be clearly seen. The two final columns of Table 2 are mean lengths of the two distributions to the right of the length-frequency plots. These mean lengths are consistent from month to month. The table shows that there are actually two series of mean lengths: one beginning at 86.7 cm in September and continuing through columns 2 and 4 of the mean lengths, and the other beginning at 84.5 cm in April (the estimate of 92.7 cm for March is an anomaly for which we have no explanation) and continuing through columns 1, 3, and 5. These represent two cohorts born each year about 6 mo apart in the spring and autumn. Note that each series of mean lengths continues only for about 24 mo. This is because after this time growth has slowed to an extent that it is not possible to distinguish distributions of length from different cohorts. The

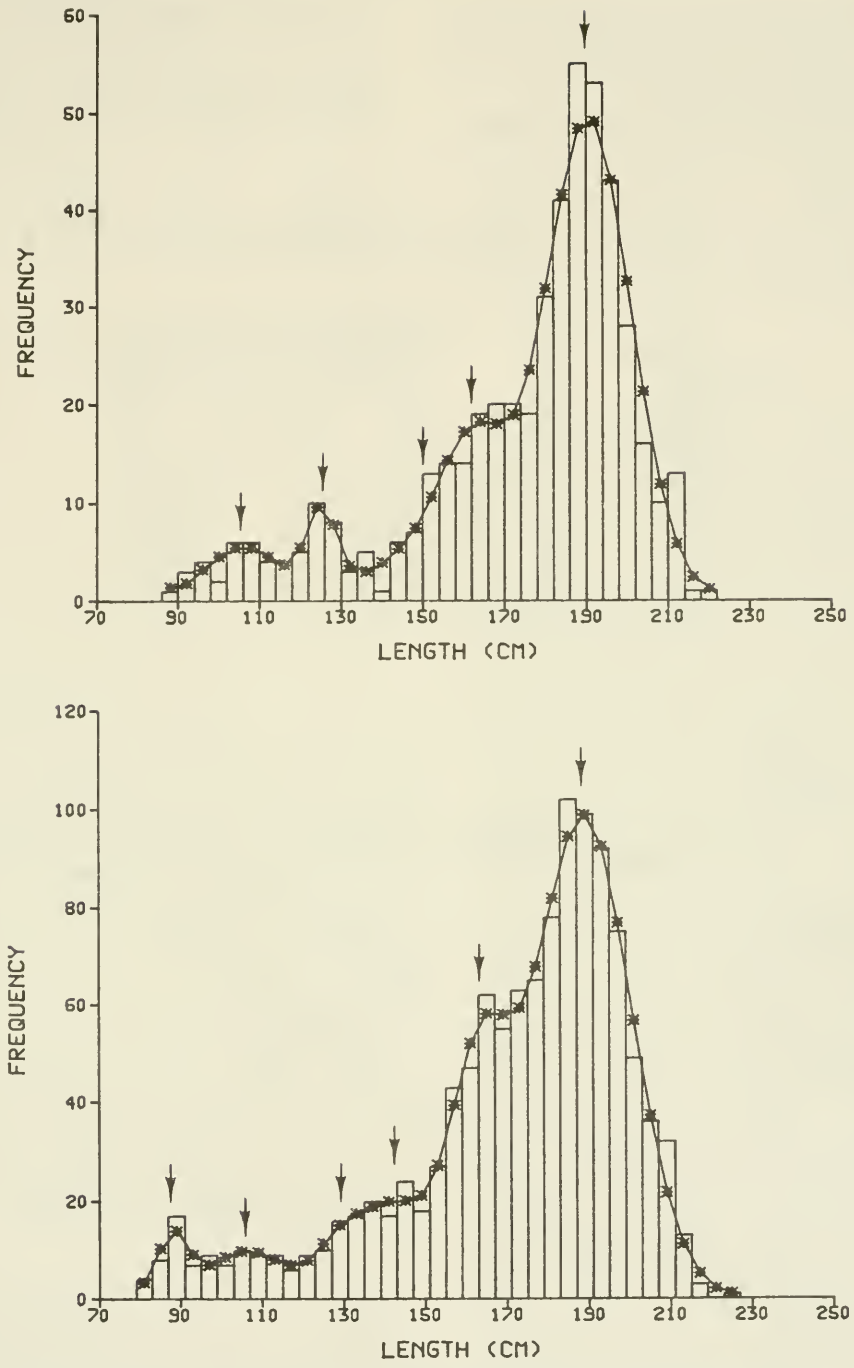

FIGURE 4.—Histograms of length and the fitted mixture of normal distributions for data for the northern offshore spotted dolphin in (A) August and (B) October. The arrows indicate the positions of the means of the fitted distributions.

mean length of 105.9 cm for June was not included in further analyses because its inclusion more than doubled the residual sums of squares for the model fit. We consider it an outlier.

Figure 5 shows Gompertz models of growth fitted separately to the mean lengths, excluding the 92.7 cm point for March, from columns 1, 3, and 5 (curve A) and, excluding the 105.9 cm point for June, from columns 2 and 4 (curve B) of Table 2. Time at birth and lengths at 1 and 2 yr were calculated as

TABLE 2.—Mean lengths of the fitted normal distributions for the northern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)					
September	536		86.7	105.0	129.4	161.3	186.9
October	1,159		87.9	106.3	129.4	142.7	163.1	188.8
November	616		91.9	113.9	129.6	145.7	159.4	187.7
December	223		97.5		127.7	149.9		187.4
January	2,926		102.9		142.4		161.9	187.4
February	2,772		104.1		140.7	151.8	161.5	186.3
March	866	[1]92.7	113.2	131.4			160.7	188.7
April	700	84.5	113.6		146.0		163.6	188.5
May	423	84.5	108.7	133.9	147.5		165.9	187.9
June	300	90.7	[1]105.9	135.5			165.2	189.5
July	266	91.8	118.0	136.1	150.8		164.5	190.1
August	486	105.7	125.1		151.8		162.6	190.5

[1]These mean lengths were not included in further analyses.

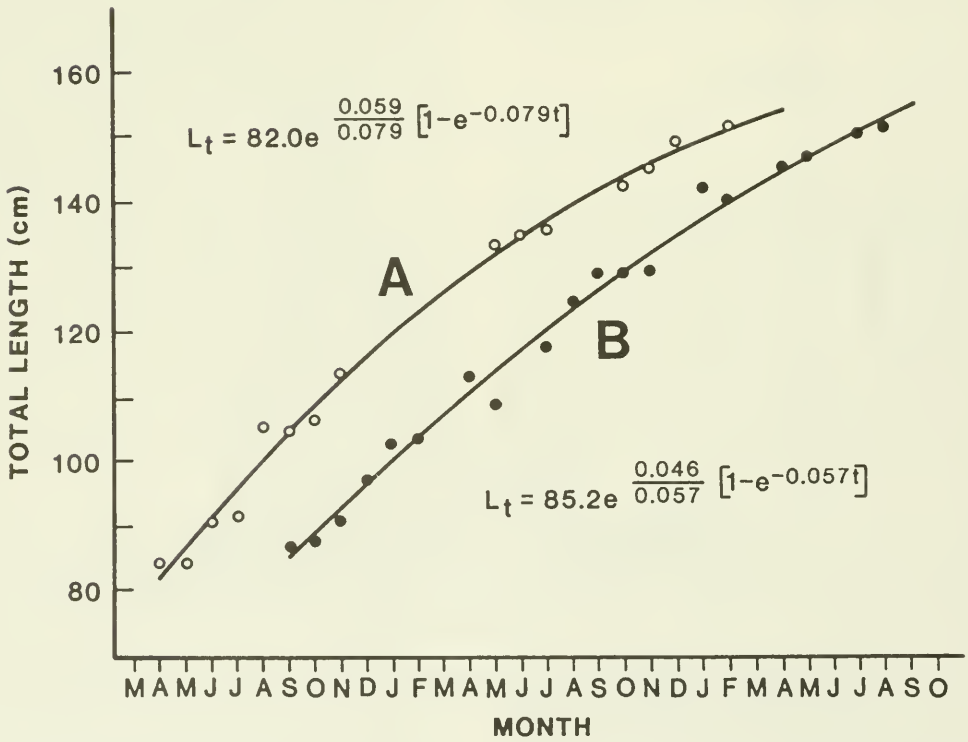

FIGURE 5.—Mean values of monthly distributions of length from data for the northern offshore spotted dolphin. The two curves represent two annual cohorts fitted separately by the Gompertz model of growth. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

described above with the following results:

	Growth curve A	*Growth curve B*
Fixed length at birth (estimated in this paper)	85.4 cm	85.4 cm
Estimated time of birth	May 9	September 11
Estimated length at 1 yr	132.6 cm	126.2 cm
Estimated length at 2 yr	154.9 cm	154.3 cm

Rates of growth as centimeters per month for the two fitted curves adjusted for length at birth are as follows:

	Rate of growth	
Months after birth	*Curve A*	*Curve B*
0	5.03	3.80
6	3.94	3.43
12	2.76	2.89
18	1.81	2.33
24	1.14	1.82

Southern Population

Table 3 shows the estimates of mean length of the fitted normal distributions for each month. For these data it is clear, apart from the mean lengths of 105.0 cm in January and 127.5 cm in May, that there is only one cohort born each year in the southern summer. As a result of this and the much smaller sample sizes, distributions of length could only be distinguished up to about 18 mo. The two final columns of Table 3 show the mean lengths of the two distributions to the right of the length-frequency plots. These are quite consistent from month to month, as with the northern data.

Figure 6 shows the Gompertz model of growth fitted to the mean lengths from columns 1 and 3 of Table 3. Time at birth and length at 1 yr were calculated as described above with the following results:

Fixed length at birth (estimated in this paper)	83.2 cm
Estimated time of birth	6 January
Estimated length at 1 yr	127.9 cm

Rates of growth for this fitted curve do not decrease from birth as they do for the northern population because the curve has a point of inflection at approximately 50 mo. The rates of growth at 0, 6, 12, and 18 mo after birth are 3.29, 3.72, 4.12, and 4.47 cm/mo, respectively.

TABLE 3.—Mean lengths of the fitted normal distributions for the southern offshore spotted dolphin.

Month	Sample size	Mean lengths of fitted distributions (cm)				
December	47	81.0		123.5	165.7	187.9
January	254	87.0	[1]105.0	131.0	164.5	187.8
February	412	85.1		134.9	165.6	188.0
March	57	90.0		139.3		189.7
April	43	97.9		140.8	163.3	189.5
May	212	97.1	[1]127.5	144.3	157.7	182.6
June	42	99.0			163.8	185.3

[1]These mean lengths were not included in further analyses.

Discussion

There are several sources of variability in the estimates of mean length by month to which the growth models have been fitted. There is individual variation in time of birth, length at birth, and growth rate. The calving season may vary from year to year and area to area. The specimens which were measured are subject to the usual sampling variation. Sampling in a particular year may not have been random with respect to time in each month. Given these sources of variability, it is interesting that the results should appear so consistent.

The growth curves were fitted to the unweighted mean lengths. If the variation in the mean length of a distribution is considered to be due largely to sampling error, then there is a justification for a weighted regression. We believe that this is not necessarily the case and that the unweighted regressions represent the best descriptions of growth for these data. When weighted regressions were performed the fitted curves changed negligibly.

The most important potential problem is that the method relies upon being able to analyze a sample of data in which reproduction is seasonal and in which the timing of seasonality is constant. This analysis has shown that this may be difficult to achieve. Only by stratification of the data by area could consistent results be obtained. Stratification of the data by area improves the consistency of the series of mean lengths because offshore spotted dolphins appear to have different calving seasons depending upon the area of capture. In probability, this seasonality is not actually a function of area but of schools or groups of schools which tend to inhabit different areas with different environmental conditions. Thus, even with the best stratification scheme, there may always be asynchronous seasonal elements in a sample of data from any given area affecting the estimation of the mean lengths of the cohorts.

In this analysis we pooled the data from several years for our monthly samples, rather than attempt-

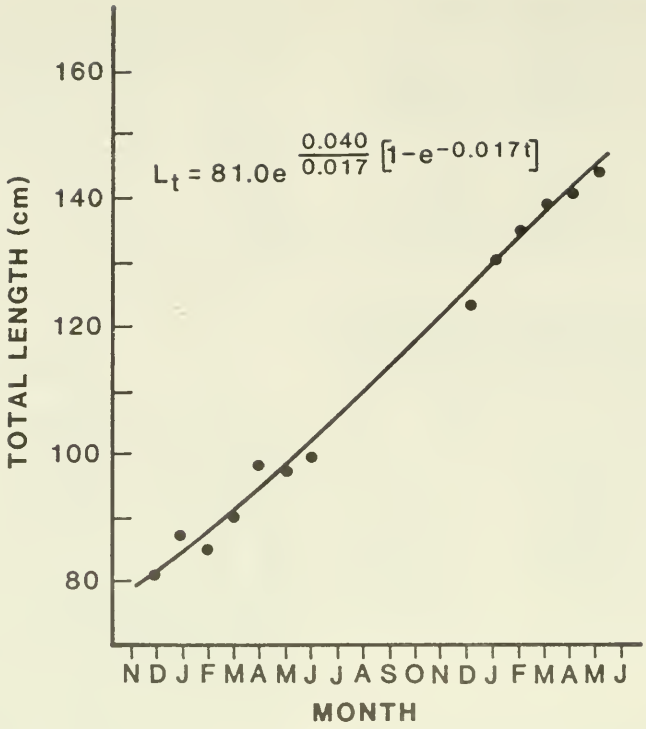

FIGURE 6.—Mean values of monthly distributions of length from data for the southern offshore spotted dolphin. The curve represents one annual cohort fitted by the Gompertz model of growth. The open circles were not included in the fitting of the curve. NOTE: The equations were fitted using relative time and are not therefore accurate models of growth. To obtain such growth models, relative time can be converted to absolute time using the estimate of length at birth and the equation refitted to these data.

ing to follow actual cohorts of animals from individual years as did Perrin et al. (1976) in their analyses. Combining the data from several years introduces additional variation in the data if the timing of the calving season varies from year to year, but it increases sample sizes and minimizes bias caused by nonrandom timing of sampling within months. In addition, we are mainly interested in an average growth rate which is best estimated from several years of data.

Perrin et al. (1976) fitted a linear model to mean lengths estimated in the months of October 1972, January, February, March, and April through June 1973 from which they extrapolated to obtain an estimate of length at 1 yr of 147.5 cm for the northern offshore spotted dolphin. The authors recognized that this estimate was biased upwards because growth rates of delphinids do decrease in the first year and revised this estimate downwards based on aged specimens. We believe our analyses to be more accurate than those of Perrin et al. (1976) and our results to be a substantial improvement.

Barlow (1984) found an indication of two peak calving seasons for spotted dolphins north of the Equator, in the spring and autumn, but that the animals were born throughout the year. South of the Equator he found a single season peaking around April. These results are similar to ours but the timing of the southern season does not agree. The difference can be explained by Barlow's use of Perrin et al.'s (1976) growth curve which predicted a mean length of 138.0 cm for 1-yr-old animals. Our growth equations predict animals of this length to be from 14 to 16 mo old.

The two growth curves fitted to the mean lengths from the two cohorts in the northern region predict different lengths-at-age and are characterized by very different growth rates. It is possible that these two cohorts actually grow at different rates because of environmental factors, but we believe that the dif-

ferences are more likely a result of variability in the data. We suggest, therefore, that the mean of the estimates from both growth curves be used for estimates of lengths-at-age for the northern offshore spotted dolphin.

For the southern population, the mean lengths of 105.0 and 127.5 cm for January and May, respectively, suggest that there may be two calving seasons in this area. At present, the sample size is too small to assess whether or not this is the case.

ESTIMATION OF LENGTH-AT-AGE USING GROWTH-LAYER-GROUP (GLG) AGING

Increments of tissue are deposited in teeth as a function of time. The most important incremental pattern in odontocete teeth is comprised of growth layer groups (GLGs), defined as "a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentine, cementum, or bone which is defined as a countable unit" (Perrin and Myrick 1980, p. 48-49). These GLGs are used for age determination in many species of odontocetes, as well as pinnipeds and sirenians (see review by Scheffer and Myrick 1980), but in most species no calibration of GLGs with absolute time is available. However, a few known-age captive and minimum-known-age captive bottlenose dolphins (Sergeant 1959; Sergeant et al. 1973; Hui 1978) and captive tetracycline-marked specimens of other species (*Lagenorhynchus obscurus*, Best 1976; *Delphinus delphis*, Gurevich et al. 1980; *S. longirostris*, Myrick et al. 1984) have provided evidence that the GLG as defined and calibrated by these workers represents an annual deposition pattern. In the absence of any known-age specimens of spotted dolphins, we have assumed that a GLG pattern similar to that described in the above species represents the same amount of time.

Methods

A sample of 800 males and 800 females, selected randomly from the specimens collected between 1973 and 1978, and all 312 female specimens collected in 1981 made up the sample of animals from which teeth were aged.

The teeth were decalcified in RDO[4], a commercial decalcifying agent, cut longitudinally into 24 μm thin sections using a freezing microtome, stained in haematoxylin, and mounted in 100% glycerin. Detailed procedures for the preparation technique and interpretation of GLGs are described by Myrick et al. (1983).

Teeth from each of the 1,600 specimens collected between 1973 and 1978 were "read" for age at least three times, to the nearest 0.1 GLG in young animals, by each of two readers over a period of 2 yr. The series of age estimates was averaged for each reader, and the resulting two mean age estimates were again averaged to produce a pooled mean age estimate (see Reilly et al. 1983). Only one age reading was made by each reader for the 312 specimens collected in 1981, and the mean of these two readings determined. For lack of a preference for one reader's estimates, growth rate analyses used the pooled mean and mean age estimates. Growth models were fit to the age-length data for males and females separately.

Growth rate was estimated by regressing length on number of GLGs (age) using Laird's (1969) form of the Gompertz model. The data were truncated at ≤3.0 GLGs in order to reduce the effects of older animals on our estimates of growth in the first 2 yr, in case the chosen model failed to describe growth adequately over a wider range of ages. Length at birth was fixed at the independently estimated value of 85.4 cm (see above).

Results

There was no difference in growth between males and females at this age. Therefore, the data were pooled. Figure 7 shows the Gompertz model of growth fitted to the pooled data. The model gives a predicted length of 123 cm (SD = 0.7 cm) at 1 yr and a predicted length of 143 cm (SD = 0.6 cm) at 2 yr. These standard deviations are underestimates because they do not incorporate variability in the age of individual specimens resulting from between reader differences.

Figure 7 also shows that lengths predicted by this model may be underestimated up to about 8 mo and overestimated from about 8 to 13 mo. For comparison with predicted length at 1 yr from the model, the mean length of specimens aged between 0.9 and 1.1 yr (n = 24) is 121 cm with a range of 101-140 cm.

The estimated monthly growth rate is 3.84 cm/mo initially, falling to 3.11 cm/mo at 6 mo, 2.33 cm/mo at 12 mo, 1.67 cm/mo at 18 mo, and 1.15 cm/mo at 24 mo.

Discussion

The accuracy of these length-at-age estimates

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

depends upon the representativeness of the sample, the accuracy of the readings, the assumptions that 1 GLG equals 1 yr, and the adequacy of the growth model.

The sample analyzed was a simple random sample, stratified only by sex, taken from all specimens collected between 1973 and 1978. These were themselves a sample of the animals killed incidental to fishing operations, which were a sample of the population. Although Powers and Barlow (fn. 2) have shown a bias towards a higher proportion of calves killed in purse seine nets, we have no reason to believe that the relationship between length and age is different in our sample than in the population.

Teeth were read as accurately as possible. Reilly et al. (1983) have investigated the precision of the readings but, without known-age animals, it is not possible to validate their accuracy.

Our assumption that 1 GLG equals 1 yr is based on captive, tetracycline-marked Hawaiian spinner dolphins (Myrick et al. 1984) a distantly related species. Known-age, captive or marked spotted dolphins are not available for direct GLG calibration. If differences are found between GLG in spotted and spinner dolphin teeth when data from known-age spotted dolphins are available, these estimates of growth based on GLGs will need to be revised.

It is often assumed that when one GLG is deposited each year the first GLG begins with the neonatal line immediately at birth and ends precisely 1 yr later. Yet it is possible, as suggested by Perrin et al. (1977) for *S. longirostris*, that the first GLG is not always complete. Teeth from young, known-age dolphins from the same stock born at different times during the year are needed to address this question.

It is also possible that the neonatal line may not be deposited immediately at the time of birth. In bottlenose dolphins, stranded on the mid-Atlantic coast of the United States, variability has been found in the time of deposition of the neonatal line in 18 neonatal specimens (Hohn unpubl. data). These specimens were identified as neonates because they lacked the umbilicus (indicating that the calf was not stillborn) and their dorsal fin and flukes were folded (Tavolga and Essapian 1957). Some of these stranded specimens showed no neonatal line while others had part of a neonatal line deposited. Similarly, in our sample of offshore spotted dolphins from northern areas there is not neonatal line in some postnatal specimens so that the amount of time since birth is unknown. This difference in timing of neonatal line deposition may be due to individual variation in tooth growth and mineralization or small difference in gestation time.

The precise timing of the deposition of the first

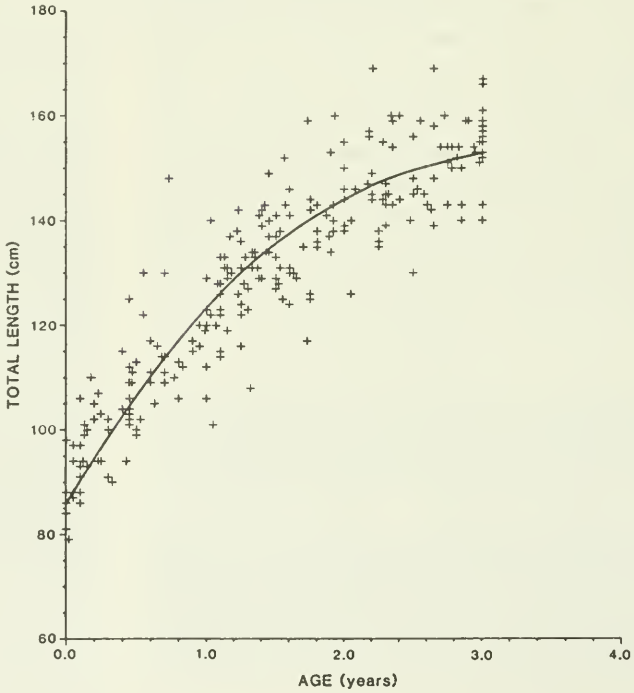

FIGURE 7.—Length-age [GLGs, (growth layer groups), pooled mean estimates] data for northern offshore spotted dolphins up to 3.0 GLGs, and the fitted Gompertz model of growth.

GLG (beginning with the neonatal line) is important in estimates of age in young animals. For a specimen estimated to be 0-yr-old based on GLGs but which is known not to be a neonate, the age must necessarily be an underestimate of the actual age of that specimen, and, consequently, the average length of "0-yr-olds" would be greater than the average length of new-born specimens. When the Gompertz model (with L_0 not fixed) is fitted to the age data, the predicted length at age 0 is 89.6 cm, 4.2 cm higher than the length-at-birth estimate. The age at which the predicted length is 89.6 cm when L_0 is fixed at 85.4 cm is about 0.1 GLGs. This indicates a possible bias of about 0.1 GLGs for young animals. However, this difference between predicted length for fits of the model with fixed and floated L_0 diminishes rapidly and at 0.7 GLGs predicted length is 114.0 cm for both models.

The Gompertz model appears to be generally suitable in describing the early growth of the offshore spotted dolphin based on GLG readings. However, the pattern of points around the fitted line in Figure 7 up to about 1.1 GLGs indicates that growth during this period may not be adequately described by a single curve. This pattern may be a result of either sampling variation or errors in reading, but it may be due to changes in growth rate during this period resulting from changes in food intake. Perrin et al. (1976) have estimated that weaning occurs at about 11 mo in the offshore spotted dolphin so that during the period from about 8 to 13 mo, milk intake will be decreasing and the intake of solid food will be increasing. Growth rates may well reflect these changes. If this is the case, a two-cycle model may describe growth more accurately during this period. Such an approach was used by Perrin et al. (1976, 1977) in spotted and spinner dolphins, respectively, to describe a secondary surge in the growth of pre-adult animals.

CONCLUDING REMARKS

Our analyses have produced different estimates of growth rates and lengths-at-age from two different techniques. The reliability of fitting growth curves to series of means of identifiable distributions of length by month depends primarily upon being able to select a sample in which breeding is both seasonal and synchronous from year to year. The reliability of fitting growth curves to length-age data as determined by counting GLGs depends primarily upon the validity of the assumption that 1 GLG is equivalent to 1 yr. We believe that neither technique is sufficiently reliable to be labelled as the "best" method or to try to calibrate the other. Rather, our analyses underline the need for the analysis of data collected from known-age animals of these populations. However, we do believe that the estimates of growth rates and lengths-at-age presented here are the best currently available for offshore spotted dolphins from the eastern tropical Pacific.

ACKNOWLEDGMENTS

Teeth were prepared by P. Sloan, M. Kimura, and D. Stanley. Age determination readings were made by A. Myrick and the first author. J. Barlow offered advice on growth models and W. Perrin made suggestions during the course of the analyses. Most of the illustrations were prepared by R. Allen. R. Hankins and S. Chivers were particularly helpful in data editing, computer programming, and some data analysis. We would like to thank R. Brownell, Jr., D. Chapman, F. Hester, and D. Siniff and colleagues at the SWFC and IATTC, especially J. Barlow, D. DeMaster, A. Myrick, W. Perrin, M. Scott, and A. Wild for critical reviews of an earlier version of the manuscript.

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FACTORS AFFECTING THE GROWTH OF UNDERSIZE WESTERN ROCK LOBSTER, *PANULIRUS CYGNUS* GEORGE, RETURNED BY FISHERMEN TO THE SEA

R. S. Brown and N. Caputi[1]

ABSTRACT

The Western Australian fishery for the western rock lobster, *Panulirus cygnus*, yielded about 12,400 t, valued at $A100 million, in 1982-83. It is the largest single species fishery in Australia and one of the largest rock lobster fisheries in the world.

During a season, between 16 and 20 million undersize rock lobsters are brought aboard the vessels by normal fishing operations, despite the escape gaps in all professional and amateur pots. All undersize animals must be returned by fishermen to the sea, but to accomplish this it took from a few minutes to hours, depending on the sorting technique used. The negative effects of handling on the survival of the undersize lobsters have been previously reported, but another important aspect is the effect of handling (damage, exposure, and displacement) on the growth rate of returned undersize rock lobsters.

Two laboratory experiments showed that growth increment at the first molt after air exposure was significantly reduced, and in one of the experiments it was also significantly reduced for the second molt after exposure.

Three field tagging trials were conducted with 6,700 undersize rock lobsters. One trial showed that exposure had a significant detrimental effect; the other trial in which exposure was tested, there was a negative, but not significant, trend. Damage (number of appendages lost) and displacement from the home range significantly reduced the growth increment in each of the three tagging trials. The growth increment of damaged animals was inversely proportional to the number of appendages lost by the animal with sizes ranging from 0.33 to 0.48 mm smaller per appendage missing. The losses to the fishery and other associated problems caused by the reduced growth of the undersize lobsters are discussed.

The fully exploited stocks of western rock lobster, *Panulirus cygnus* George, support the largest single species fishery in Australia and one of the largest rock lobster fisheries in the world, averaging 10,000 t for the last 9 yr to 1982-83. In 1982-83 the fishery recorded its best season; the 12,400 t worth about $A100 million, were landed by 780 boats licensed to participate in the industry. The amateur catch from the fishery, estimated at 1.6% of the professional catch (Norton 1981), is considered to be a relatively insignificant component of the total fishery, though it may be locally important and occurs in shallow areas where large numbers of undersize rock lobsters (i.e., those with a carapace length <76 mm and referred to below as undersize) are caught.

Fishing pressure on the rock lobster stock has been increasing steadily during the past 20 yr, even though it has been a limited entry fishery since 1963 (Morgan 1980a, b; Hancock 1981). This has led to the need for constant monitoring of the fishery and the updating of management procedures and regulations to ensure the stability and viability of the rock lobster stock (Bowen 1980; Morgan 1980a, b; Hancock 1981; Morgan et al. 1982). An important component of management of a fully exploited stock is to reduce waste, e.g., by predation and poor handling techniques.

Two of the most important regulations that aid in conservation of the western rock lobster stock pertain to undersize:

1) Compulsory use of a 54 × 305 mm escape gap in each of the 76,000 professional and all amateur pots (traps) in the fishery allows many undersize animals to escape before the pot is pulled (Bowen 1963).
2) Undersize lobsters that do not escape and are brought aboard must be returned to the sea.

Although use of escape gaps reduces the retention of undersize lobsters by over 50% (Bowen 1963; Brown unpubl. data), between 16 and 20 million undersize animals are still handled each season by professional fishermen (Brown and Caputi 1983). The latter authors found that the handling practices of fishermen, which cause exposure, damage

[1]Western Australian Marine Research Laboratories, Department of Fisheries and Wildlife, P.O. Box 20, North Beach 6020, Western Australia.

Manuscript accepted December 1984.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

(number of legs and antennae missing), and displacement of undersize lobsters, resulted in a drop in recapture (mainly due to mortality) of 14.6%. After allowing for the natural mortality expected before the undersize lobsters would reach legal size, the effective reduction that could be expected was 11.4%. For the 1982-83 season, the loss to the fishery could have been in the vicinity of $A8 million.

An aspect of undersize lobster mortality and loss of commercial production that was not discussed by Brown and Caputi (1983) concerns the effect of handling on the growth of these animals. If the growth rate of the undersize lobster is reduced by exposure, damage, and displacement, then it could affect the rock lobster stock and the commercial fishery in a number of important ways as discussed by Davis (1981): 1) The time taken for undersize lobsters to reach legal size would be increased; 2) these animals would enter the commercial fishery at a smaller size than those with unhindered growth; and 3) the size at which these animals would attain maturity would be reduced.

Other researchers have shown that the growth rate of crustaceans generally and rock lobsters in particular is affected by a variety of environmental factors such as food availability, temperature, photoperiod, molt phase, injuries, shelter availability, salinity, and others (Chittleborough 1974a, 1975, 1976; Aiken 1980). Far less information is available on the effects of commercial and recreational fishing practice on the growth rates of exploited rock lobster or other crustacean populations (Davis and Dodrill 1980; Davis 1981). Information that is available deals almost exclusively with the injury (damage) component of fishing activities or experimentation. Injury, recorded as the loss of appendages, has been shown to affect significantly the growth of rock lobsters *P. cygnus* (Chittleborough 1975) and *P. argus* (Davis 1981) and the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes* (Kuris and Mager 1975).

This paper reports effects of three major components of the capture and release experience (i.e., damage, exposure, and displacement) on the growth rate of undersize lobsters caught from commercially fished populations of *P. cygnus*. The effect of the various components was examined by tagging lobsters that were exposed for various periods and were displaced at different distances from their place of capture, with any damage being recorded. Growth of experimental animals between release and subsequent recapture was compared with that of control lobsters which had not been exposed, damaged, or displaced. Laboratory experiments were also conducted in which undersize lobsters were exposed for various periods and their growth rates subsequently monitored over the next two molts.

Consequences to the industry of any reduction in growth rate are discussed in the light of results from this research and the findings reported by Brown and Caputi (1983).

LABORATORY EXPERIMENTS

Materials and Methods

Exposed undersize lobsters were maintained under otherwise near optimal growing conditions of excess food, adequate shelter, and protection from potential predators (see also Chittleborough 1975) and their molt increment and intermolt period compared with those of unexposed animals.

Undersize lobsters (72-75 mm carapace length) were collected from the field and transported in aerated seawater tanks to the laboratory in January 1978. Each animal was examined for size, sex, and damage. Sixty undersize lobsters with no damage or maximum of one appendage missing were selected and marked with numbered squares of Dymo Scotch Tape,[2] fixed to the dorsal side of the carapace with Repco Super Glue and placed in open circulation seawater tanks. Aquaria were checked daily for molts, and animals were fed to excess on whole live mussels and fresh fish. If molting had occurred, the exuvia was removed and the newly molted animal left for a week to harden before measuring and renumbering. In January 1979, each animal was allowed to undergo a minimum of two molts before the entire group (Group I, consisting of 4 subgroups of 15 animals) was given exposures of 0, 15, 30, or 60 min at a temperature of 34°35°C. Animals that died prior to exposure were not replaced.

After exposure, undersize lobsters were returned to their tanks and were checked daily for any molts or deaths. Feeding and renumbering was continued as for pre-exposure. Every animal that survived was allowed at least two molts before the experiment was terminated.

A second group of undersize lobsters (Group II, consisting of 5 groups of 12 animals), collected in June 1978, were treated in the exact manner as described for Group I with the exception that exposures of 0, 15, 30, 60, or 120 min at 20°21°C took place 18 mo later, in December 1979.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

In the January 1979 exposure experiment (Group I), all eight undersize animals exposed for 60 min died before the second molt after exposure, while one animal died from each of 0-, 15-, and 30-min exposure categories leaving 7, 10, and 7 animals respectively.

An analysis of variance on growth increment at the first molt after exposure showed that exposure was significant ($P < 0.01$) after other factors (e.g., sex, damage, initial size), which may have affected growth, were taken into account. However, at the second molt after exposure, the effect of exposure on growth increment was not significant ($P > 0.05$). An analysis of variance on the time taken (days) between the last molt before exposure and first molt after exposure (intermolt period) resulted in exposure being not significant. Exposure was also not significant for the following intermolt period.

In the December 1979 exposure experiment (Group II), one animal died in the 0-, 15-, 30-, and 120-min exposure categories and two died from the 60-min exposure before the second molt after exposure. In this experiment, exposure had a significant effect on the growth increment for both the first ($P < 0.001$) and the second ($P < 0.01$) molts after exposure. An analysis on the intermolt period for the first molt after exposure showed no significant effect due to exposure, but exposure was significant ($P < 0.05$) for the following intermolt period, mainly due to the low number of days between molts for animals in the 120-min exposure category.

TAGGING TRIALS

Materials and Methods

There are two main events in the commercial fishery for *P. cygnus* which follow molting by a large proportion of the population. The first event is in November-December when maturing 4-5 yr old pale-shelled animals known locally as "whites" move offshore into deeper water, where the breeding stock is generally situated. During the "whites" fishery, about 40% of the total catch is taken (Morgan 1980b). The second event is in March-April when postmolt, dark-shelled, sedentary animals called "reds" are captured (George 1958; Morgan 1977). As already mentioned in Brown and Caputi (1983), account had to be taken of these two periods when planning tagging trials as the migratory "whites" could be more mobile and in a physiologically different state than nonmigratory "reds" and hence their growth could be affected differently by handling practices (i.e., causing exposure, displacement, and damage). With these possible differences in mind, three tagging trials were conducted at Two Rocks, Western Australia (lat. 31°29.7′S, long. 115°31′E), avoiding the period of the full moon, when catches are at their lowest (Morgan 1974, 1977): 1) migratory "whites" phase—26 November to 10 December 1978; 2) nonmigratory "reds" phase—19 February to 10 March 1979; and 3) migratory "whites" phase—16 November to 9 December 1979.

An area consisting of shallow limestone reefs (6-18 m depth) within 6 km of shore and stretching from Two Rocks Marina to the mouth of Moore River was fished with standard wire beehive pots without escape gaps (Bowen 1971; Morgan and Barker 1974). Pots were baited daily with a variety of fresh fish; heads of Australian salmon, *Arripis trutta*; and bullock hocks.

Tagging Trial A

An experimental area was established, consisting of a grid on which pots were set and undersize lobsters could be displaced distances of 0, 230, 460, 910, 1,370, and 1,830 m from a base line of experimental pots where they were captured (Brown and Caputi 1983). Pots were pulled each morning during the trial, weather permitting. Undersize (66 to <76 mm) lobsters were tagged with a numbered western rock lobster tag (Chittleborough 1974b) and their carapaces measured to the nearest 0.1 mm. Also recorded was the animal's damage, sex, and the depth and bottom type where it was caught and released. Grid areas were generally fished only once to avoid recapturing previously tagged animals. Recaptures of tagged animals were made by commercial fishermen who were paid a reward for the tag and market value for the animal if it had molted to legal size. See Brown and Caputi (1983) for complete details of experimental procedures. Number of releases for this trial was about 1,500.

Tagging Trial B

Procedure for trial B was the same as trial A except that the 1,370 m transect was not set and exposure categories of 0, 30, 60, 120, and 180 min were also examined. Exposed undersize lobster were placed in plastic prawn baskets (lug baskets; commonly used by fishermen to sort their catch) and exposed to air for the desired period before release at one of the displacement transects. About 2,300 tagged animals were released.

Tagging Trial C

Similar procedures were followed as for trials A and B, but only the 1,830 m and a new 3,660 m transects were set and exposure categories of 0, 15, 30, 60 min were used. Because parasite infection was observed on some animals (6.3% of releases), its presence was recorded as it could affect growth. The infection is a combination of a fungus (*Fusarium* sp.) and a bacteria (*Vibrio* sp.), which causes black lesions in the exoskeleton, usually in areas that have been damaged (e.g., tail fans and appendages). Infections were scored on an ordered scale of 0-6, with 0 indicating no infection. About 2,900 tagged animals were released.

Results

Figure 1 shows mean size (carapace) increment related to month of recapture for each of three tagging trials. In tagging trials A and C (November-December releases), February was the first month when there was evidence of molting in animals recaptured (Fig. 1); therefore, subsequent analyses on size increment only used recaptures from February onwards. In tagging trial B (February-March releases), May was the first month when there was evidence of molting (Fig. 1), so only data from this month onwards was used for the analyses.

The results of an analysis of variance (ANOVA) on size increment for each of three tagging trials is shown in Table 1. In this analysis recapture month, sex, color, displacement, and exposure were treated as factors while size at release, damage, and level of parasite infection were treated as covariates. The analysis enables the significance of these factors and covariates to be determined after effects of other factors and covariates are taken into account.

In tagging trial A, after taking the effects of other factors into account (e.g., sex, recapture month, etc.), the size increment per appendage missing was smaller by 0.48 mm with standard error of 0.04. This is also evident from Figure 2 which shows the relationship between mean size increment and numbers of appendages missing for all recaptures from February to June 1979. Size increment in tagging trial C was also smaller by 0.48 mm per appendage missing with standard error of 0.004 (see Figure 3), while that for tagging trial B was 0.33 mm smaller (standard error of 0.07).

From the ANOVA, size increments of displaced compared with nondisplaced animals were smaller by 0.32, 0.65, and 0.27 mm for tagging trials A, B, and C respectively.

Exposure in tagging trial C, after other factors were taken into account by the ANOVA, resulted in increments smaller by 0.83, 1.34, and 2.30 mm for 15-, 30-, and 60-min exposure respectively, when compared with the zero exposure category. This can also be seen from Figure 3 which shows the mean size increment for animals recaptured after February 1980 related to exposure and number of appendages missing. While the effect of exposure on growth was not significant for the February-March 1979 trial B, size increments were smaller by 0.62 and 0.73 mm for 30- and 60-min exposures respectively, compared with unexposed animals.

Mean size increment of males was larger than females by 0.95, 1.34, and 0.76 mm for the three tagging trials. Although the size at release of all animals was between 66 and 76 mm, there was still a highly significant decrease in size increment due to size at release of 0.25, 0.36, and 0.20 mm for every 1 mm increase in size at release. Difference in color, i.e., dark-shelled vs. pale-shelled animals, was significant in tagging trial A with pale-shelled animals having a greater size increment by 0.65 mm, but this was not evident in tagging trial C. In tagging trial C, level of parasite infection of the animals was found to have had a detrimental effect on growth.

DISCUSSION AND CONCLUSIONS

Exposure

Exposing undersize rock lobsters to the atmosphere was detrimental to their growth increment at the first molt after exposure in both laboratory and field tagging trials. In the December laboratory experiment (Group II) the effect of exposure was still significant at the second molt after exposure. Tagging trial B (February-March 1979) resulted in exposure not having a significant effect on growth despite the presence of a negative trend between exposure and size increment. This may have been due to the fact that only 7 of the 110 animals recaptured in May-June 1979 had been exposed; this is the period when many of the undersize lobsters would have undergone their first postexposure molt (Fig. 1). Since there is a closed season from 1 July to 14 November, no recaptures were made until the time of the second postexposure molt in November-December 1979, by which time the combined effects of two molts may have masked the effect of the exposure treatment. However, this was not the case in tagging trial C (November-December 1979), which was held at the start of the fishing season, where the effect of exposure on the first molt which occurs

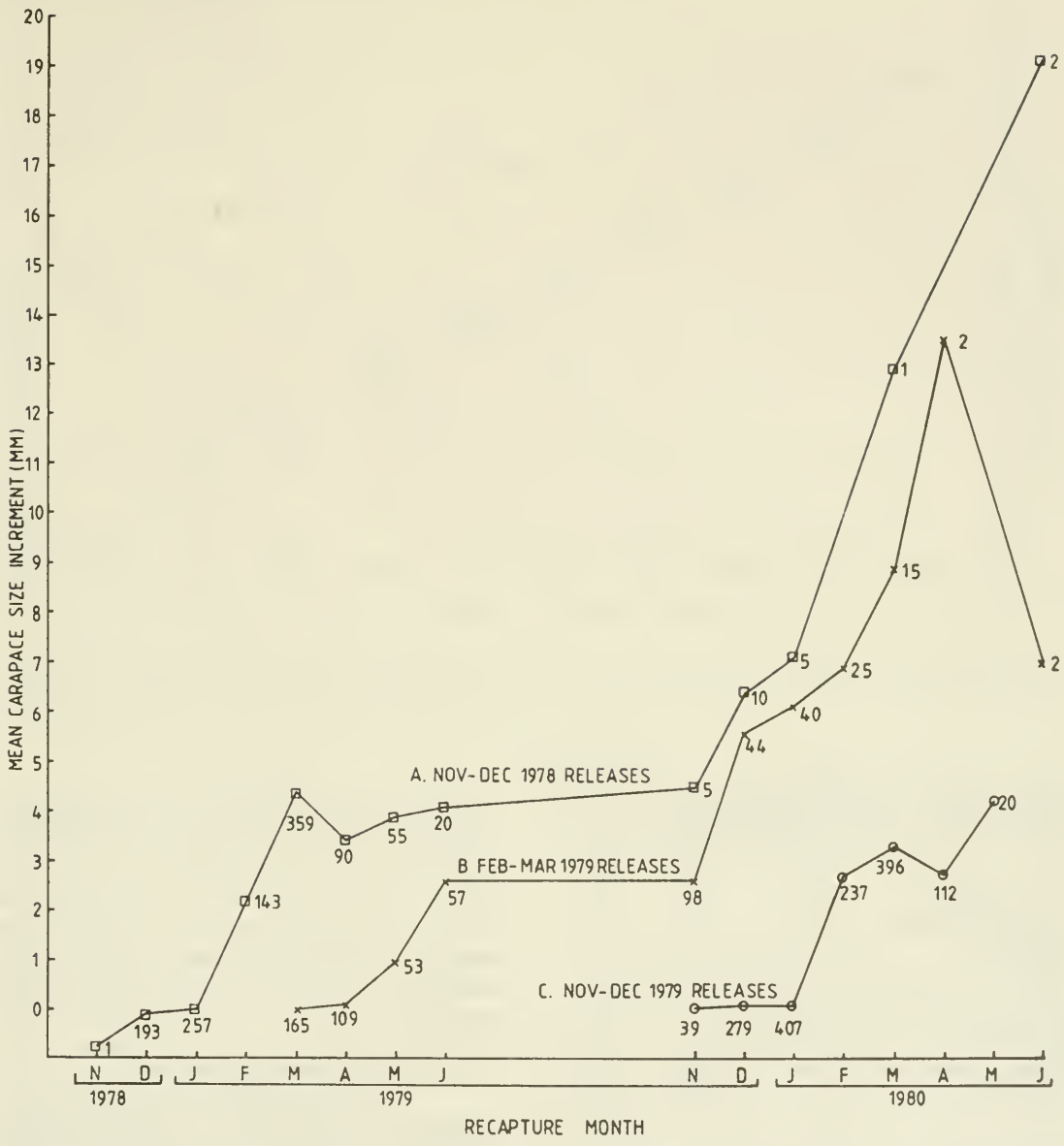

FIGURE 1.—The mean size (carapace) increment by month of recapture and the sample size involved in calculating it shown next to the points, for the three tagging trials at Two Rocks.

around February was clearly evident in animals caught from February 1980 onwards (Fig. 3, Table 1).

Damage

Damage to undersize rock lobsters was clearly shown to have a detrimental effect on growth (Table 1), which was directly proportional to the level of damage (Figs. 2, 3).

Chittleborough (1975) found that growth increment of *P. cygnus* was reduced under laboratory conditions when four or more legs were removed and repetitive loss of two or more limbs led to precocious molting with reduced molt increments leading to an overall reduction in growth. Davis and Dodrill (1980) and Davis (1981) undertook research on the effect of injuries (limb loss) produced by amateur and professional fishermen and natural causes (e.g., predators, molting accidents, etc.) on the growth rate of *P. argus* populations in the wild. They found that

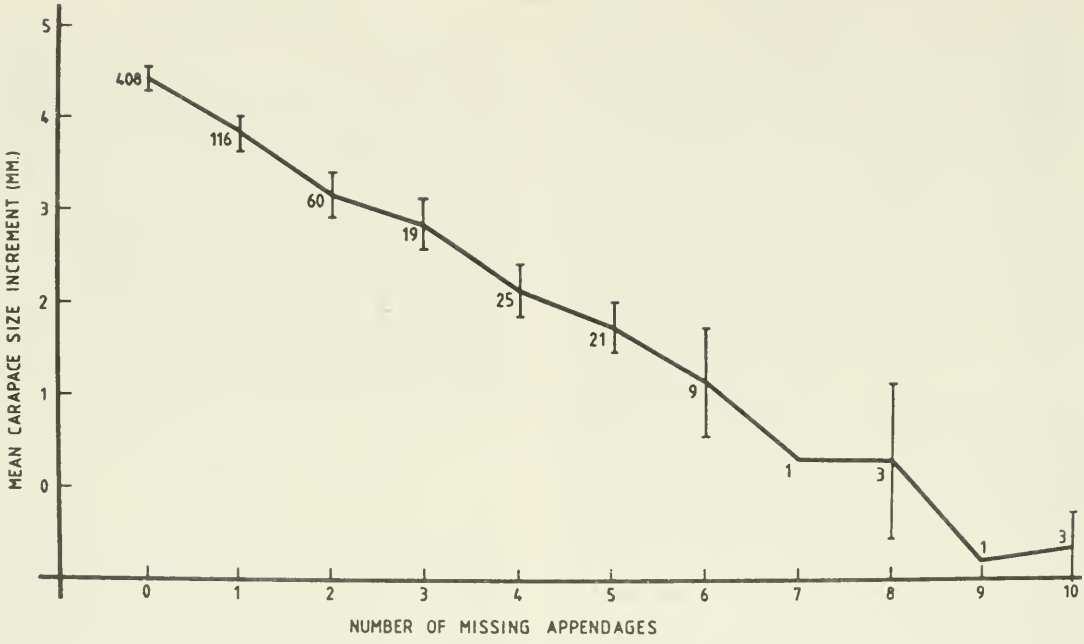

FIGURE 2.—Two Rocks, November-December 1978. The relationship between the mean size increment and number of appendages missing for recaptures from February to June 1979, with the sample size and standard error from the mean shown at each point.

TABLE 1.—The results of the analysis of variance on size increment for the three tagging trials at Two Rocks with the level of significance denoted by: NS, *, **, *** meaning not significant, $P < 0.05$, $P < 0.01$, and $P < 0.001$ respectively, and NA means not applicable.

Factor/covariate	Nov.-Dec. 1978	Feb.-Mar. 1979	Nov.-Dec. 1979
No. missing appendages	***	***	***
Displacement	*	*	*
Exposure	NA	NS	***
Recapture month	***	***	***
Sex	***	***	***
Size at release	***	***	***
Color	**	NA	NS
Parasite infection	NA	NA	***
Sample size	687	335	636

the growth rate of injured animals was significantly lower than that of uninjured animals, due to reductions in molt increment and an increase in intermolt period. Their research did not demonstrate any proportional relationship between the degree of injury and the degree of molt increment depression as had been shown for *H. oregonensis* and *P. crassipes* (Kuris and Mager 1975) and also in this study on *P. cygnus*. Davis (1981) stated that growth rate of *P. argus* with minor injuries, five or fewer appendages missing, was almost identical to the growth rate of more seriously injured animals that were missing up to nine legs and both antennae.

Displacement

The displacement of undersize rock lobster was also found to significantly affect size increment in each of the three tagging trials. This was probably due to movement of animals from their home range (Chittleborough 1974c) which could have interrupted their normal feeding behavior and thus may have contributed to a decrease in food intake and hence growth.

Overall Effect

In general the handling of undersize rock lobsters by fishermen which causes them to be exposed to the atmosphere, damaged and displaced beyond their home range, not only affects their survival (Brown and Caputi 1983) but also affects growth of those that survive. As discussed in Davis (1981), this reduction in growth may result in:

1) The undersize lobsters staying below the legal size for a longer period than necessary with some being subject to natural mortality in this extra period before entering the fishery.
2) Those animals which do enter the fishery would do so at a reduced size, hence harvestable yield would be reduced.

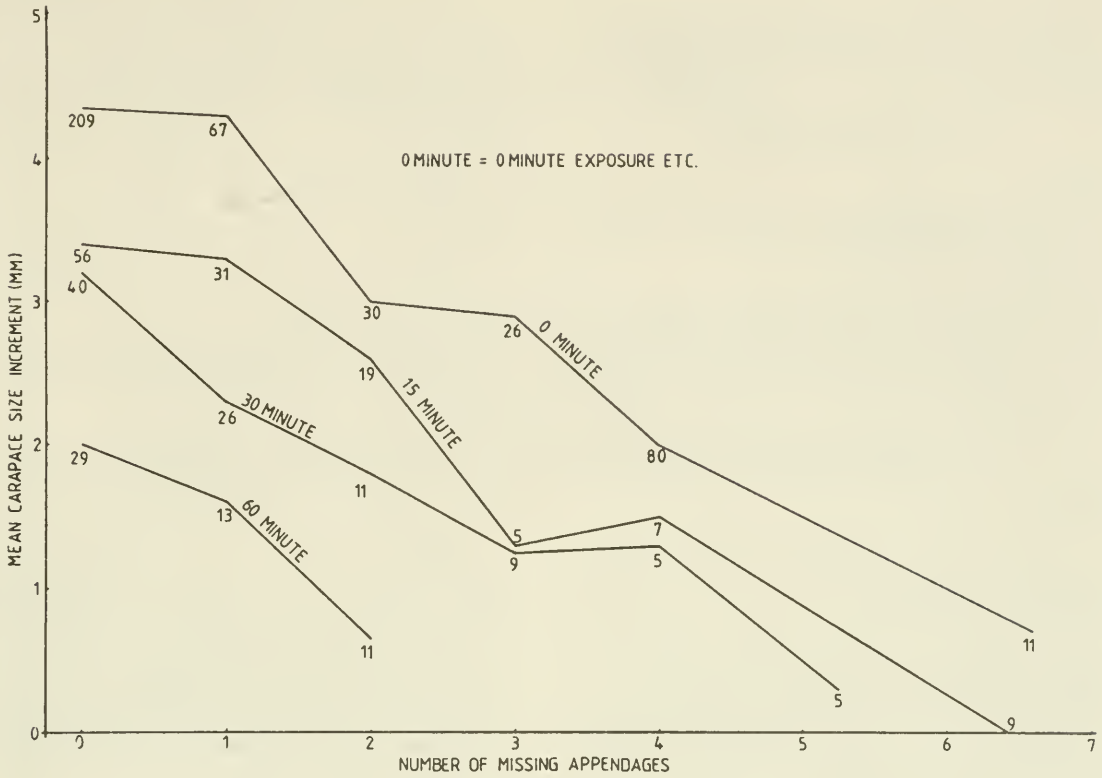

FIGURE 3.—Two Rocks, November-December 1979. The mean size increment related to exposure categories and number of missing appendages for animals recaptured from February 1980 onwards. Exposure and missing appendages categories with less than five individuals have been combined and are plotted at the mean appendage level. The sample sizes are shown next to the points.

3) Size of these animals on reaching maturity would also be reduced, which would cause a decrease in fecundity directly proportional to their reduced size (Morgan 1972). The time they would take to reach maturity would probably not be affected since age appears to determine maturity rather than size (Chittleborough 1974d).
4) Affected animals would remain undersize for longer, thereby increasing the possibility that they could undergo multiple capture and handling. Multiple handling would result in increased mortality and further reduced growth.

These factors, when added to the estimate of 14.6% reduction in recapture rate (most likely due to mortality) of the returned undersize lobsters during the fishing season (Brown and Caputi 1983), constitute a serious loss to the fishery. In addition, any mortality and reduced growth which may occur as a result of lifting the animals to the surface and returning them to the sea would also need to be added to the above loss. This loss could not be quantified as both experimentals and controls in the tagging experiments experienced this.

As mentioned by Brown and Caputi (1983), use of more effective escape gaps and an education program to encourage fishermen to return their undersize rock lobsters immediately to the sea while their vessel remained in the immediate vicinity of where the pot was pulled would help to overcome this serious source of industry created wastage. Both these approaches are currently being examined with a view to reducing the numbers of undersize lobsters that are handled and the time they are kept on board the vessels.

ACKNOWLEDGMENTS

The authors would like to thank J. Prince and J. Jenke for technical assistance during this work; Ron Duckrell, the skipper, and the crew of the *Flinders* for assistance during the tagging trials; D. A. Hancock and N. Hall for critically reading the manuscript and offering many helpful suggestions; and

M. Isaacs for typing the manuscript. This research was supported by a grant from the Australian Department of Primary Industry's Fishing Industry Research Trust Account.

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SEA SCALLOP FISHING IMPACT ON AMERICAN LOBSTERS IN THE GULF OF ST. LAWRENCE

G. S. Jamieson[1] and A. Campbell[2]

ABSTRACT

Damage to American lobsters, *Homarus americanus*, in Egmont Bay and off Miminegash, Price Edward Island, is minimal from the drags of the seasonal sea scallop, *Placopecten magellanicus*, fishery. During May 1981, when commercial sea scallop fishing was occurring, American lobster abundance was low in areas of profitable scallop exploitation. Sea bed substrate in these areas was generally smooth and most lobsters were able to avoid the gear. In the areas with and without commercial scallop fishing, 1.3% and 11.7% of observed lobsters, respectively, were injured or retained by the drag. Lobster abundance in the areas commercially exploited for scallops in May and June was significantly greater in July than in May, but whether this was a result of a natural seasonal movement of lobsters or the cessation of scallop fishing is unclear.

Sea scallop, *Placopecten magellanicus*, and American lobster, *Homarus americanus*, populations are fully exploited in Northumberland Strait, Gulf of St. Lawrence (Wilder 1947, 1965; Robinson 1979; Jamieson et al. 1981c; Campbell and Mohn 1983). Individual fishermen frequently fish both species, commonly in the same general area, although the fisheries are separated temporally (Jamieson et al. 1981c; Conan and Maynard 1983). Recently, localized low abundance of these important, commercial species has heightened long-held convictions by fishermen of the negative impact of sea scallop fishing on American lobster stocks. Fishermen's concern became acute for the Egmont Bay area during 1980, coincident with the discovery and exploitation of new nearshore scallop concentrations near West Point, Prince Edward Island (Fig. 1). Decreased scallop recruitment in recent years (Jamieson et al. 1981b, c) has resulted in a scarcity of scallops in traditional fishing areas, causing increased exploration for commercially exploitable scallop concentrations.

The magnitude of scallop gear-lobster interaction is dependent on the spatial and seasonal distributions of scallops and lobsters and the impact of scallop gear on commercial lobster abundance where the distributions of both species overlap. Scallops are widespread in Northumberland Strait (Caddy et al. 1977), but commercial concentrations are found only in limited areas. The precise locations of these areas are undocumented, and since they vary with time, they cannot be predicted with any accuracy. However, commercial log data has shown the broad distribution of scallop concentrations in Northumberland Strait during 1979-80 (Jamieson et al. 1981b, c).

The seasonal abundance and distribution of commercial-sized lobsters is largely unknown, but their general distribution overlaps that of scallops (Stasko et al. 1977; Conan and Maynard 1983). There have been few field studies conducted on lobsters in this area: Templemann (1933, 1934, 1935, 1936) reported on lobsters and the fishery in Northumberland Strait; Wilder (1963) and Wilder and Murray (1956) reported on movements and growth of tagged lobsters liberated in Egmont Bay.

Scallop and Irish moss, *Chondrus crispus*, drags can damage lobsters, although lobsters exposed on open ground tended to avoid moving drags. Most gear-induced damage has resulted from lobsters in burrows being hit or crushed by rocks disturbed by the drag (Scarratt 1973, 1975; Pringle and Jones 1980).

Investigations reported here document 1) the scallop drag/lobster interactions off Miminegash, Prince Edward Island, during August 1978 and in Egmont Bay during May and July 1981; and 2) the relative abundance and movement of lobsters trapped and tagged in Egmont Bay prior to (June-July 1981) and during the lobster fishing season (10 August-10 October 1981). Lobster abundance may change relatively rapidly because of their potential high mobility. Therefore it is important to characterize lobster microdistribution and assess the con-

[1]Department of Fisheries and Oceans, Fisheries Research Branch, Halifax, Nova Scotia; present address: Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada.
[2]Department of Fisheries and Oceans, Atlantic Biological Station, St. Andrews, New Brunswick, E0G 2X0, Canada.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

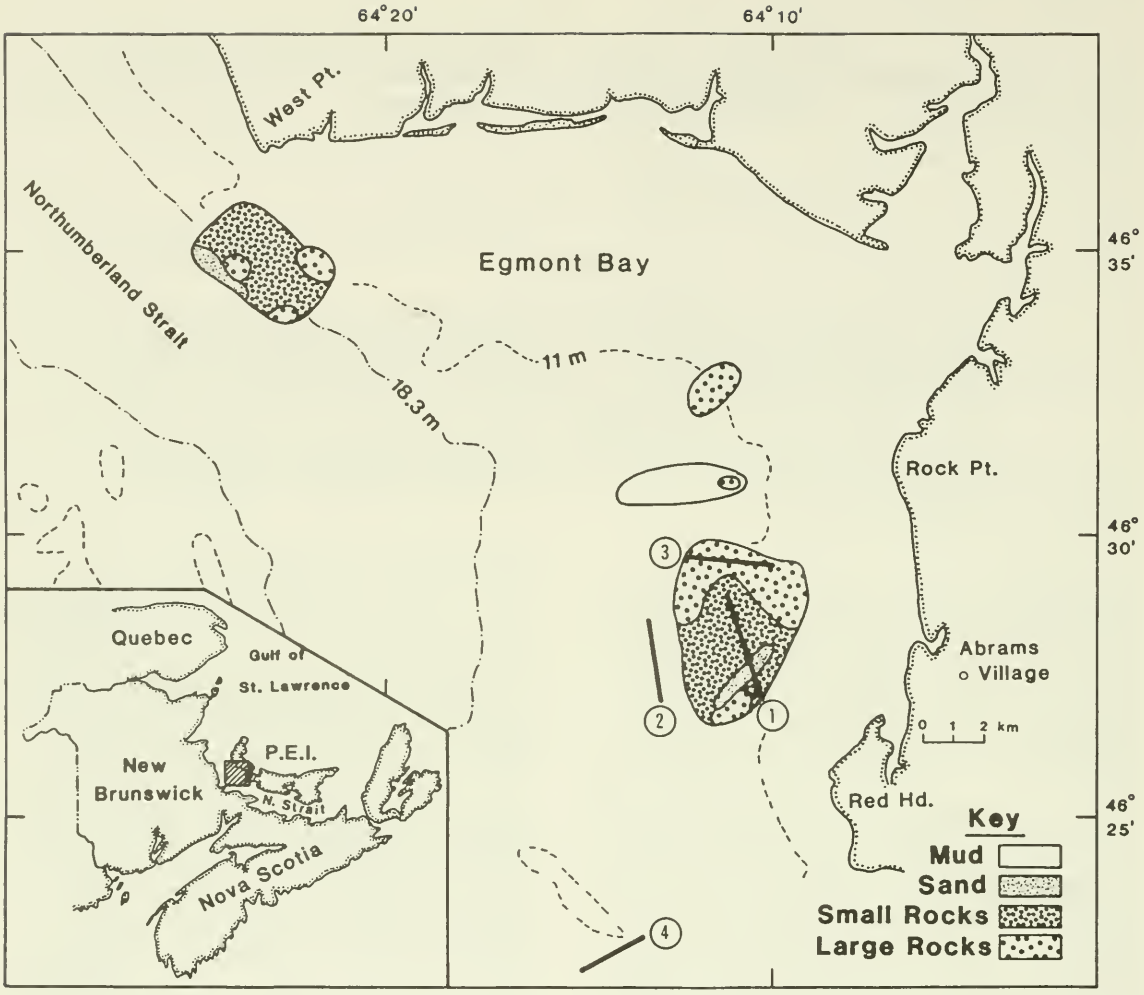

FIGURE 1.—General substrate type as observed by divers in the areas surveyed in Egmont Bay, Northumberland Strait, Gulf of St. Lawrence. Locations of stations (heavy lines) sampled for lobsters in Egmont Bay, Northumberland Strait: 1 = recently heavily fished scallop ground, 2 = recently lightly fished scallop ground, 3 = no recent scallop fishing (large rocks), 4 = no scallop fishing (deeper water).

sequences of scallop fishing on the degree of species overlap. Scallop fishing may directly damage lobsters, or because of the disturbance of the sea bed by the drags, may cause lobsters to avoid or be attracted to the overall area.

METHODS

Scallop Gear-Lobster Interactions

1978 Study

The interaction between three types of scallop gear and lobsters was observed by divers between 15 and 30 August 1978. The study area was in 14 m of water about 1 km from shore (long. 46°52′30″W, lat. 64°14′00″N), and consisted of a sandy bottom with occasional small rocks. The gear used was a two-gang, toothed Gulf rock drag (60 cm buckets) (Fig. 2); a two-gang Digby rock drag (76 cm buckets, no teeth) (MacPhail 1954); and a 152 cm Gulf sweep chain drag. A Gulf sweep chain drag is a smaller, lighter revision of an offshore scallop drag (Bourne 1964). A hood of 38 mm stretch mesh was placed over the drags extending to a height of 81 m above the sea bottom, and one of the buckets (half the chain sweep drag) had a similar mesh hood on the outside of the back of the drag (back cover). The bucket, or portion of the drag, without a back cover had a mesh liner. Two divers hung onto each drag during tows,

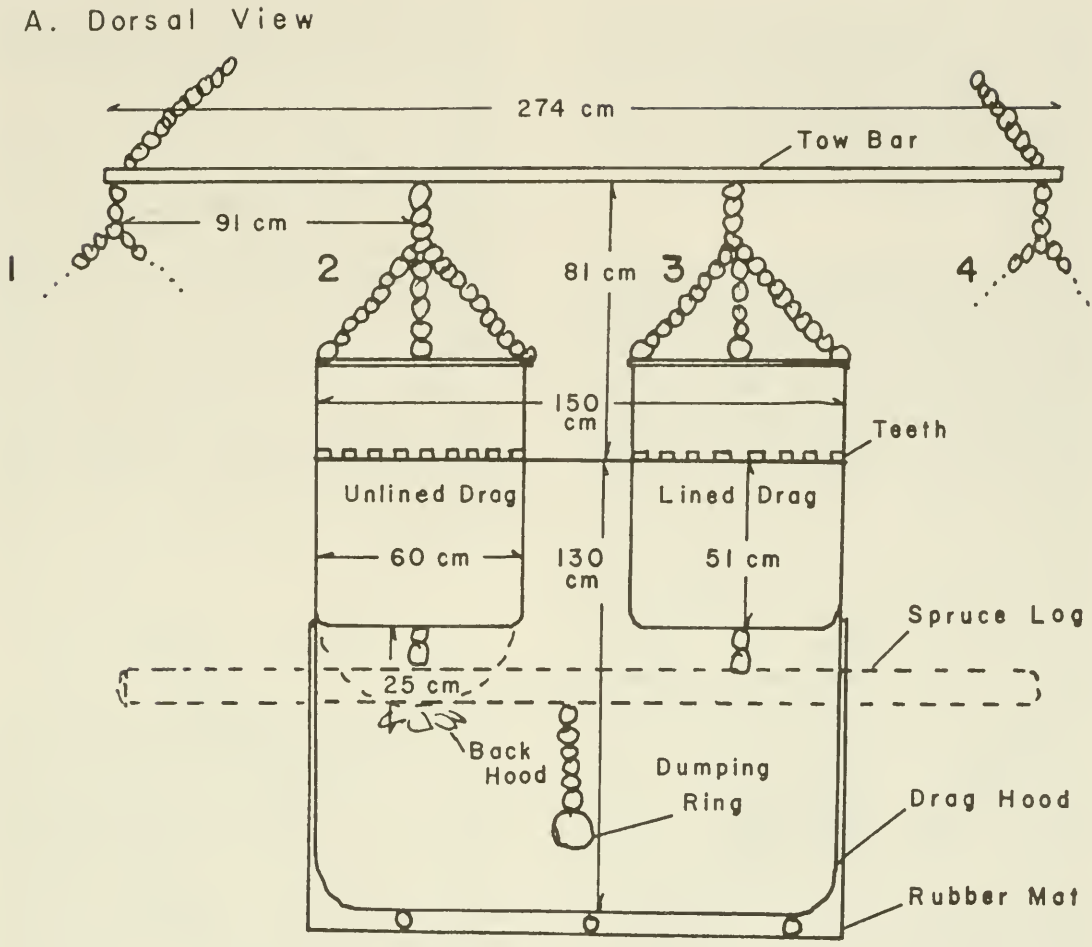

FIGURE 2.—Schematic drawings of a four-gang Gulf rock drag: (A) hood and liner arrangements used with buckets 2 and 3 in 1978 (buckets 1 and 4 were removed). In 1981, 4 unmodified buckets were used. (B) Lateral view of bucket 2 used in 1978.

noting lobster behavior and the physical effect of the drag on lobsters; carapace lengths (CL, back of eye socket to posterior carapace margin) of fished lobsters were measured. Tow velocities, established by engine rpm, were similar to commercial operations and tow duration was 5 min.

1981 Study

Dragging was conducted during 14-22 May and 27-31 July 1981. Four general areas (Fig. 3) were surveyed in both periods. Scallops and lobsters were known by fishermen to exist in areas A and A′ but scallop fishing had not occurred for several years; five research tows were conducted in May and three tows in July. Areas B and C were reported by fishermen to be prime lobster ground where scallop fishing had occurred recently or was in progress during the study; 30 research tows were conducted in May and 25 tows in July. Tow locations were randomized within an area and the number per area was arbitrarily assigned according to the apparent distribution of commercial effort in the scallop fishery. Bottom water temperatures averaged 8.8° and 18.4°C in May and July, respectively. A four-gang Gulf rock drag (Fig. 2) with 51 cm buckets was used throughout the study. Scallop rings had 69-75 mm and 80-84 mm inside and outside diameters, respectively. Lead ropes 30 m long were attached to each end of the 2.36 m club stick at the back of the drag to define an area behind the drag to be surveyed by divers. Before the drag was dropped, the lines were let out while the vessel was steaming or drifting to establish an unfished control area for survey

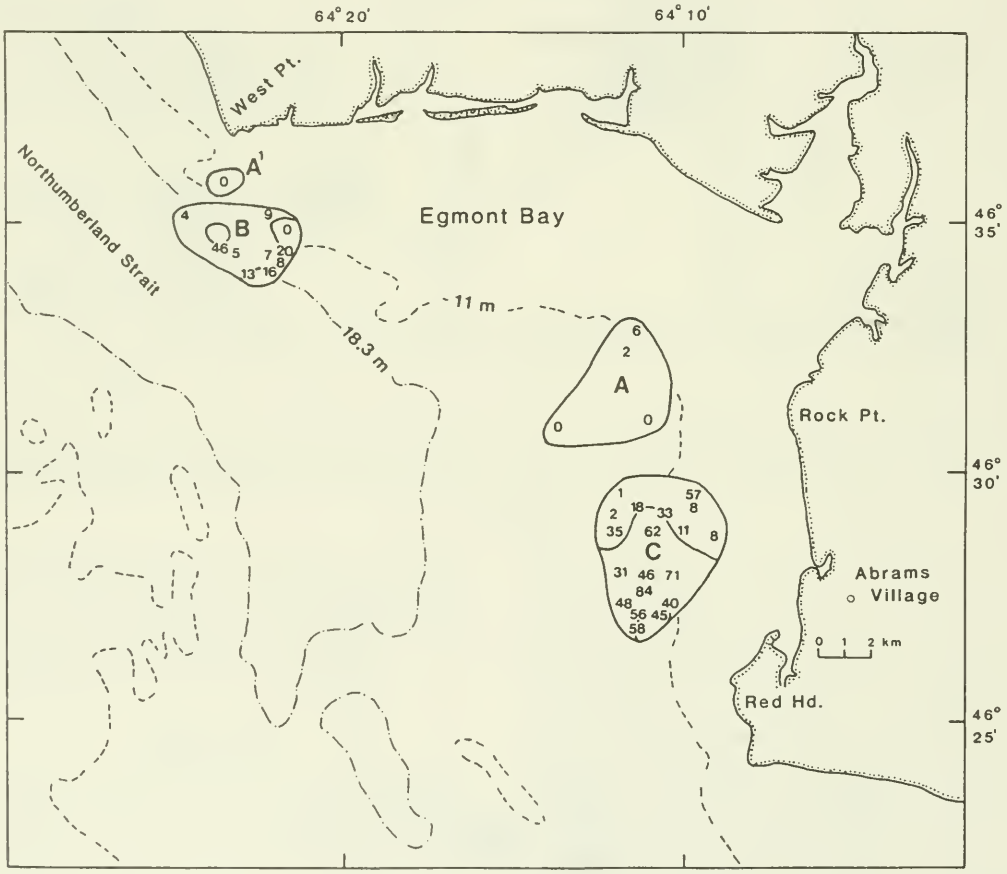

FIGURE 3.—Number of scallops fished/tow (average length = 975 m) by the gear in May in Egmont Bay, Northumberland Strait, Gulf of St. Lawrence. Identified areas are where both scallops and lobsters exist in commercial densities: A and A′ were areas where no scallop fishing had occurred for several years (= unfished control); B and C were areas where scallop fishing had recently occurred or was in progress during the study. Substrate type is shown in Figure 1.

by the divers when the drag was finally lowered. When the drag was on the bottom, divers swam along the outside edge of each lead line with a 2 m rod, noting all scallops and lobsters encountered in the 2 m wide unfished "path" (120 m^2). The divers then positioned themselves on the drag and noted the number of lobsters in the drag path during the tow, which covered on average 975 m (SD = 221). When the tow terminated, the divers searched the drag path between the lead lines (70.8 m^2) and collected the scallops and lobsters encountered. Scallop height (edge of hinge to distal edge of the valves) and lobster carapace lengths were measured to the nearest millimeter with a measuring board and vernier calipers, respectively. Location (loran C readings), bottom type (Fig. 1), water temperature, and marine plant presence were noted. Tow distance and speed were calculated from loran C readings (Jamieson 1982) and averaged 4.6 kn (SD = 1.9) in May and 4.3 kn (SD = 1.7) in July. Average tow duration was 6.9 min.

Lobster Abundance and Distribution

Four study areas (Table 1; Fig. 1) were located by loran C and were selected after bottom types were characterized from scuba diving observations. The areas were 1) recently heavily fished scallop ground, 2) recently lightly fished scallop ground, 3) ground with large rocks with no recent scallop fishing, and 4) typical lobster ground in waters deeper than areas 1-3 with no scallop fishing. Fifty, three bow, single kitchen and parlor design lobster traps with 121 mm diameter entrance ring and 31-34 mm lath spaces were set in each area. Each trap was baited with salted gaspereau (or alewife), *Alosa pseudoharengus*, and/or Atlantic herring, *Clupea harengus harengus*. The traps were set in groups, two traps per buoy, within a 1 km radius of the center of the area (Table 1). The mean interval between trap hauls from 22 June to 30 July was 3 d (1-7 d range). Each trap was reset as close as possible to the original site of each trap set.

The sex and carapace length (CL in mm) of each trapped lobster was recorded. Once a week, the terminal quarter of a pleopod endopodite was removed with scissors from each of 70-140 lobsters of various size groups, and placed in a vial containing seawater. The pleopod method described by Aiken (1973) was used to determine the molt stage of each lobster.

The bottom and surface water temperatures were recorded for each area and time fished. To observe lobster movement and growth, a total of 2,002 lobsters (ca. 500 lobsters/area) were measured and tagged (Table 1) with a sphyrion tag (Scarratt and Elson 1965) and returned to the water within 10 min and 0.5 km of the capture site. During the 10 August-10 October fishing season, lobster samples were obtained at-sea from commercial lobster fishing boats at a number of locations within and near areas 1-4.

One-way analysis of variance was used to compare the mean number of lobsters per trap haul in each area during a 1-wk sampling period and to compare the mean distance moved for lobsters from the different study areas.

From tagged lobsters recaught during the study, movement and direction statistics of tagged lobsters were analyzed by methods Jones (1959) and Saila

TABLE 1.—Summary of Egmont Bay lobster tagging experiment, 22 June-30 July 1981.

Details	Area 1 Heavily fished scallop ground	Area 2 Lightly fished scallop ground	Area 3 Scallop ground with rocks[1]	Area 4 Lobster ground[1]
Location				
Latitude (°N)	46°28′	46°27′	46°28′	46°23′
Longitude (°W)	64°10′	64°13′	64°12′	64°15′
Bottom type	mud, small rock (<10 cm)	mud, small rock (<10 cm)	mud, rocks (>10 cm)	mud, rocks (>10 cm)
Mean depth (m)	11	13	11	18
No. of traps	50	50	50	50
Trap soak-over (days) (range)	2-5	1-7	2-5	1-5
No. of trap hauls	489	568	500	591
No. of lobsters caught	2,507	1,967	2,568	2,330
Total tags released	500	501	500	501
Total tags returned[2]	182	162	234	162
% of total tags released in area[2]	36.4	32.3	46.8	32.3

[1]No scallop fishing.
[2]Number of tags returned up to 30 October 1981 including tags without recapture locations.

and Flowers (1968) have reported, using a computer program by Campbell et al. (1983).

RESULTS

Scallop Gear-Lobster Interactions

1978 Study

No scallops were present but lobsters were numerous and were observed by divers to be frequently foraging in the open. Average carapace length of 22 diver-collected lobsters was 61.3 mm (SD = 26.8). While the microdistribution of substrate type was patchy, tows were of sufficient duration to cover all substrate types. Under the assumption of an average uniform lobster density during tows, lobster catches made by the Gulf sweep-chain drag over sand and rock-sand were highest. Average catches in the lined and unlined portion of the drag were 0.53 and 0.07 lobsters/m of drag width fished per min ($m^{-1}min^{-1}$), respectively (Table 2).

No lobsters were retained by the unlined rock drags, but since they were retained in the back cover of the drag, lobsters were entering the drag and passing through the rings. These lobsters did not show any external evidence of damage. The hoods of all three drag types contained lobsters, indicating that lobsters can escape by swimming over the advancing drag.

TABLE 2.—Average number of lobsters caught $m^{-1}min^{-1}$ of drag width in the hoods and linings of the scallop gear used in 1978. Each drag type was hauled over both sand and sand-rock substrates off Miminegash, Prince Edward Island. L = lined gear; UL = unlined gear; H = hood; B = back cover.

Drag type	No. tows	Lobster catch			
		L	UL	H	B
Gulf sweep chain	5	0.53	0.07	0.15	0.31
Gulf rock drag	5	0.11	0.00	0.06	0.11
Digby rock drag	6	0.02	0.00	0.07	0.04

1981 Study

RELATIVE SCALLOP AND LOBSTER ABUNDANCE.—Catch results and sightings per tow (Jamieson et al. 1981a) indicated that for each study area, considerable variation existed in abundance of both scallops (Fig. 3) and lobsters (Fig. 4). Substrate type was variable over the distance of a single tow, and this appeared to be a major factor influencing relative scallop and lobster abundance.

Scallop and lobster densities in the two areas (B and C) fished for scallops varied significantly on some dates (Table 3) from those densities in the nonfished areas (A and A[1]); fished grounds had a greater number of scallops, but fewer lobsters, than did the nonfished ground. Between the two fished areas, the only significant ($P < 0.05$) difference was in the scallop drag catch in May, but study area C off Red Head generally yielded more of both species than did study area B off West Point (Figs. 3, 4).

There were no significant differences ($P > 0.05$) in the densities of either scallop or lobster in the nonfished area between the two sampling periods. Lobster sightings per tow in both fished areas were significantly greater ($P < 0.05$) in July than in May, but the number of sightings averaged less than in the unfished area. Although not always significant, the general seasonal trend of lobster abundance, as indicated by the control sampling procedures, increased between May and July in all areas. Scallop catch decreased significantly ($P < 0.01$) in the ground off Red Head between May and July. On fished ground, average scallop density decreased whereas scallop density on the nonfished ground increased during this time period.

TABLE 3.—Average scallop and lobster catch in a 4-gang Gulf rock drag in 1981, and the abundance per 1,000 m^2 in each study area before the scallop drag was towed (control) and in the drag path behind the drag. Values with asterisks are significantly different from the corresponding value in the nonfished scallop location. * = $P < 0.05$; ** = $P < 0.01$; n = number of tows.

Location	Month	Control density				Drag				Drag path			
		n	Scallop	n	Lobster	n	No. scallop caught	n	No. lobsters observed	n	Scallop	n	Lobster
Nonfished area	May	4	6.25	4	2.08	5	0.87	4	3.03	2	0.0	2	0.00
	July	2	12.50	2	16.67	3	0.15	3	4.62	3	4.71	3	4.71
West Point	May	4	56.23	4	0.00	11	7.59*	11	0.48	8	24.70*	8	1.76
	July	3	22.21	3	2.78*	7	10.10	7	1.48*	5	127.08	5	5.65
Red Head	May	9	99.03**	9	0.93	19	16.38**	19	0.87	12	68.25**	12	1.18
	July	9	58.31	9	5.55	18	8.34**	18	1.98*	10	52.24	10	1.41

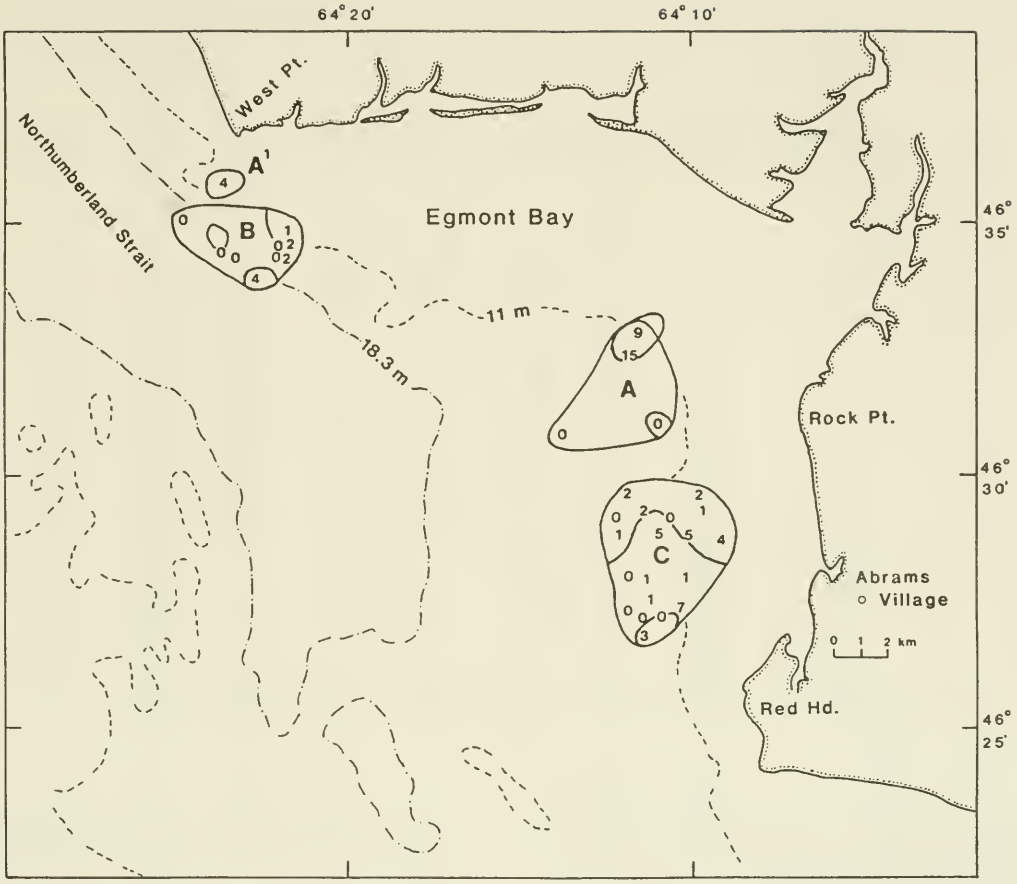

FIGURE 4.—Number of lobsters observed by divers in May during each tow in Egmont Bay, Northumberland Strait, Gulf of St. Lawrence. Substrate type is shown in Figure 1. Area designations are explained in Figure 3.

SCALLOP GEAR: LOBSTER INTERACTION.—No relation was found between the two sample periods and the number of lobsters injured or retained during a tow (Table 4). The weighted percentage of lobsters injured or retained was 11.7 and 1.3, for the nonfished and combined fished areas, respectively. Injured lobsters were not found in the drag path, although occasionally lobsters were observed to retreat into burrows in front of a moving drag. Whether they subsequently became damaged or trapped in their burrows is unknown, but the absence of damaged lobsters in the drag path suggests that the frequency of lobster damage is low on commercial scallop ground especially where there is a general lack of large rocks and boulders. However, 14 of the 30 locations surveyed had occasional large rocks.

Most lobsters encountered were too small (mean CL = 72 mm) (Table 5) to be retained by the scallop gear unless the steel rings making the drag were partially blocked by debris. All lobsters <92 mm CL can pass through a 70 mm inside diameter scallop ring (Stasko 1975). Several lobsters were seen by the divers entering the drag and passing through the rings apparently unscathed. In 63 tows, 11 lobsters were affected directly by the scallop gear: four were retained by the drag (the ring openings were block-

TABLE 4.—Frequency by month and location of lobster reduction and/or injury during dragging.

Details	Month	Nonfished areas	Fished areas	
			West Point	Red Head
No. lobsters observed	May	28	10	35
	July	32	24	82
No. lobsters injured/retained	May	3	1	0
	July	4	1	0
% injured/ retained	May	11	10	0
	July	13	4	0

TABLE 5.—Summary of lobster catches during closed fishing season (June-July 1981) and during the fishing season (August-October 1981) in Egmont Bay. Shorts = prerecruits <63.5 mm CL; legals = recruits ≥63.5 mm CL.

					Prerecruits			Recruits		
Week no.	Time period	Area	No. of lobsters sampled	No. of trap hauls	% total lobsters	No. per trap haul	% females of total shorts	No. per trap haul	% females of total legals	Mean CL (mm)
1	22-26 June	2	2	104	0	0	0	0.02	0	81.0
		4	2	96	50.0	0.01	0	0.01	100.0	72.0
2	29 June-	1	3	100	33.3	0.01	100.0	0.02	100.0	71.0
	3 July	2	17	102	29.4	0.05	80.0	0.12	33.3	68.8
		3	2	100	50.0	0.01	100.0	0.01	100.0	66.0
		4	11	100	45.5	0.05	40.0	0.06	50.0	67.3
3	6-10 July	1	141	98	9.2	0.13	53.9	1.31	20.3	71.4
		2	114	102	12.3	0.14	35.7	0.98	35.4	71.5
		3	99	100	11.1	0.11	72.7	0.88	21.6	70.9
		4	35	100	25.0	0.09	22.2	0.27	30.8	72.6
4	13-17 July	1	503	94	17.7	0.95	42.7	4.40	31.9	71.0
		2	542	104	10.4	0.59	54.1	5.06	33.8	72.1
		3	550	100	12.2	0.67	41.8	4.83	33.3	71.3
		4	395	100	9.4	0.38	45.9	3.65	31.6	72.6
5	20-24 July	1	794	99	13.7	1.10	55.0	6.92	33.9	69.9
		2	708	104	9.0	0.62	51.6	6.19	36.3	71.6
		3	840	100	10.7	0.90	47.8	7.50	36.6	70.4
		4	792	98	6.3	0.51	58.0	7.57	33.8	72.4
6	27-30 July	1	1,066	98	15.7	1.70	44.3	9.17	29.1	70.3
		2	584	52	9.3	1.04	57.4	10.19	31.0	71.6
		3	1,077	100	9.2	0.99	44.4	9.78	29.6	70.9
		4	1,095	97	6.2	0.70	39.7	10.59	32.0	73.3
8	10-14 Aug.	(1)	1,582	488	24.5	0.79	44.9	2.40	33.1	71.9
9	17-21 Aug.	(1)	155	125	47.7	0.59	46.2	0.65	(2)	(2)
10	24-28 Aug.	(1)	501	240	44.7	0.93	48.5	1.13	31.8	73.2
11	13 Aug.-									
	4 Sept.	(1)	458	245	42.5	0.80	42.6	1.07	34.4	73.0
13	14-18 Sept.	(1)	496	237	51.6	1.08	50.8	0.99	44.2	71.5
15	28 Sept.-									
	2 Oct.	(1)	129	74	7.7	1.18	53.4	0.57	(2)	(2)

[1]All fishing areas during fishing season.
[2]Size and sex not recorded

ed with *Laminaria longicruris*), four passed under the drag and were possibly injured, and three were struck during the course of one tow (in May) resulting in claw loss or a cracked carapace. In the latter instance, strong currents impeded the escape of lobsters.

Scallop size frequencies were similar in May and July in each of the two commercially fished areas and all scallop age classes were exploited about equally.

Lobster Abundance and Distribution

Abundance

The number of lobsters caught per unit of effort (trap haul; CPUE) increased during the experimental fishing period in all areas (Table 5). During the commercial fishing period, CPUE of prerecruits increased but CPUE of legal-sized lobsters decreased presumably as a result of fishing mortality. Number of lobsters per trap haul was not significantly different between areas observed during the experimental period (Table 5). The use of CPUE is unreliable in the quantitative estimation of lobster abundance as many factors affect trapability, including water temperature, lobster behavior, molting, relative trap and lobster densities, and bait attractiveness (Elner 1980).

Lobster Movement

Of the 740 tagged lobsters recaptured (37%), 658 had recapture location data (Tables 1, 6). In areas 1, 2, and 3, the majority (65-78%) of tagged lobsters were recaptured within 10 km of release, but in area 4, 50% were caught 11-18.5 km from release (Table 6). The mean distance moved was not significantly different for tagged lobsters released in areas 1, 2, or 3, but lobsters from area 4 moved a significantly ($P < 0.01$) greater mean distance than those of the other three areas.

Direction statistics (according to Saila and Flowers 1968) summarize the nature of lobster movement

TABLE 6.—Summary statistics of distance travelled and direction moved by tagged lobsters released at four areas in Egmont Bay during June-July 1981, and recaptured up to 30 October 1981. (Direction statistics calculated according to Jones [1959] and Saila and Flowers [1968] are $\bar{\Theta}$ = mean vector angle from true north; V and V′ = directed movement along north-south and east-west plane, respectively, negative values of V and V′ indicate net southerly and westerly movement, respectively; R and Z = Rayleigh test statistics for randomness or uniform distribution of points about a circle; * = significant at $P < 0.01$ indicates a non-uniform distribution.) SD = Standard deviation.

	Release area			
Details	1 Heavily fished scallop ground	2 Lightly fished scallop ground	3 Scallop ground with rocks[1]	4 Lobster ground[1]
% of total recaptures moved 0-10 km	65.2	70.3	78.2	35.3
% of total recaptures moved 11-18.5 km	28.1	16.2	19.8	49.7
% of total recaptures moved >18.5 km	6.7	13.5	2.0	15.0
Total recaptures	164	148	207	139
Mean distance moved, km (± 1 SD)	9.2 (0.5)	10.1 (0.6)	8.3 (0.4)	[2]12.9 (0.6)
Maximum distance moved, km	25.0	45.0	38.9	49.7
$\bar{\Theta}$	247.3	289.3	310.5	344.4
V (km/d)	−0.055	0.026	0.062	0.213
V′ (km/d)	−0.132	−0.075	−0.073	−0.059
R	74.9	26.3	64.9	63.5
Z	34.2*	4.7*	20.4*	29.0*

[1]Light or no scallop fishing.
[2]Value for mean distance travelled significantly different ($P < 0.01$); other values not significantly different ($P > 0.05$).

(Table 6). The Rayleigh test statistic, Z, indicated a non-uniform distribution of tag returns ($P < 0.01$) for each area of release. Results of the Rayleigh test should be treated with caution (Batschalet 1965) since there is some evidence of bimodality. In general, the returns exhibited three main directions of movement for lobsters: south-west for area 1, north-west for areas 2 and 3, and north for area 4 (Table 6). V and V′, the north-south and east-west coefficients of directed movement, measure the mean daily travel of the group. Lobsters from areas 1-3 showed little dispersion in a north-south direction in contrast to lobsters from area 4, which moved the greatest in a northward direction (0.213 km/d). Lobsters from all areas generally moved west, but lobsters from Area 1, the heavily fished scallop ground, tended to disperse furthest west per day (0.132 km/d). Dispersion to the west is perhaps largely the result of the relative proximity of the release areas to the western shore of Prince Edward Island, which restricted lobster movement to the east.

Lobster Growth

Determinations of molt stage from pleopod examinations indicated that lobsters may have molted as early as 6-12 July (Table 7). Trapability of lobsters is affected by molt stage, with late molt stages (e.g., $D_{4.0}$; Aiken 1973) being difficult to trap. The high percentage of D_3 to D_4 animals (stages just before molting) in mid-August indicated that considerable molting was imminent, and this probably affected CPUE at this time. Many tagged lobsters (47.8%, $N = 46$) recaptured during the period 24 August-26 September had molted.

DISCUSSION

The results of this study are probably area and

TABLE 7.—Percentage of pleopod stages of lobsters sampled from Egmont Bay, July-September 1981. Pleopod stages 3.0-3.5 and 4.0-5.5 predict lobsters molting within 1.9-4.0 wk and 0.3-2.4 wk, respectively, at 15°-19°C (Aiken 1973). Prediction of molting time for pleopod stage 1.0-2.5 is unreliable but usually exceeds 4.0-10.3 wk.

	% of lobsters				
	Pleopod stage				
Period	1.0-2.5	3.0-3.5	4.0-5.5	No. of lobsters	Temperature (°C)
6-10 July	97.1	1.5	1.4	69	15.5
13-17 July	98.2	0.9	0.9	113	16.0
20-24 July	96.5	3.5	0.0	142	16.5
27-30 July	89.9	6.6	3.5	117	19.0
10-14 Aug.	76.3	21.1	2.6	76	18.1
31 Aug.-4 Sept.	91.1	5.9	3.0	101	17.5

time specific. Nevertheless the extent of sea scallop gear damage to American lobsters in Egmont Bay was measured, and this permits estimation of the damage to lobsters on similar substrate types in other locations. In the nonfished area there was no significant difference in the lobster abundance between the May and July observations, whereas there were significant differences in relative seasonal lobster abundance in the fished areas. In western Northumberland Strait at the time of this study, scallop fishing occurred primarily between late April and late June, with a minor amount of fishing between mid-October and winter freeze-up (Jamieson et al. 1981c). There was limited scallop fishing during July. If lobsters were displaced by scallop dragging during May and June, normal seasonal lobster densities could be reestablished by late July. It is unclear whether the greater density of lobsters in the fished areas in July was due to normal seasonal migration onto these grounds or to the absence of scallop fishing. Data from tagged lobsters suggested that some immigration may have occurred from the deeper water areas of the Strait, but it also appeared that overall abundance on the scallop grounds may have been reduced by scallop dragging activity. Predators have been reported to be attracted to the disturbed substrate in a drag's path (Caddy 1973), but how this relates to lobsters is unclear.

The trapability of lobsters is a function of many variables (Elner 1980), making the quantification of lobster abundance difficult in the four trap study areas. There was a lower percentage of short lobsters and a larger mean carapace length in Area 4 than in the other areas (Table 5). When large lobsters were trapped there were generally fewer small lobsters in the traps (Table 5), but this may have resulted from agonistic behavior (Cobb and Tamm 1975) rather than relative density. Water temperature increases may also have affected behavior and possibly had major modifying effects on lobster growth and/or movement. McLeese and Wilder (1958) documented an increase in lobster rate of movement with increasing temperature, but what effect this had on the average direction of movement during the study period is unclear. The mean movement rate of lobsters in our study (Table 7) was similar to that reported by Saila and Flowers (1968) for mature lobsters off Rhode Island. Saila and Flowers (1968) showed that the coefficients of directed movement, V and V′, are sensitive to changes in movement patterns at various life history stages, and hence are a possible function of lobster maturity level and the sex ratio used in their calculation. These potential influences were not considered here because of limited duration of the study and the relative close proximity of release and recapture areas which were probably not optimal to permit extensive data analysis.

There probably was a directed movement of tagged lobsters from area 4 (deeper water) into Egmont Bay. This may have contributed to the increased CPUE during July-October. Templeman (1936) found there was some movement during the summer with lobsters congregating in the relatively shallow inshore water areas of Northumberland Strait and that some lobsters moved offshore in the fall. The disproportionate sex ratio of legal-sized lobsters observed in the present study suggested a geographic distributional difference between the sexes of lobsters after maturity during July-August.

Lobster trapability, and hence estimated abundance, can be influenced by molt stage. Many legal-sized lobsters appeared to have molted between August and September, and while the data are insufficient to support the fact that a molt may have occurred prior to or during the experimental fishing period (late June-July), other investigations have presented evidence in the literature that lobsters in this area do molt in late spring (Templeman 1934, 1936; Wilder 1963). If, in fact, two molts did occur during the study period, this along with increased water temperature increasing lobster movement (McLeese and Wilder 1958) could partially explain the rapid increase in CPUE during July. However, no soft-shelled lobsters were observed during July, while soft-shelled lobsters were quite frequently encountered in fishermen's traps during the August-September fishing season.

The seasonal nature of the fisheries minimizes the impact of scallop gear on lobsters because lobsters are in low abundance on scallop ground at the time of greatest scallop fishing activity. Commercial concentrations of scallops and lobsters also appear to be largely separated spatially (Figs. 2, 3). What then is the likely economic impact in Egmont Bay of scallop fishing on lobsters, and how does this compare to the value of the exploited scallop resource? No reported commercial scallop fishing was reported in 1980 off Red Head, but vessel logs recorded that 1,509.4 kg of adductor muscle meat were taken near West Point (scallop log areas 77 and 78 combined, Jamieson et al. 1981c). Average CPUE was about 2.4 $kg/h \cdot m^{-1}$, indicating that 629 $h \cdot m$ of effort was expended. In our study, a total of 8.2 $h \cdot m$ of research effort was expended in May on the fished grounds and 22 lobsters were observed behind the drag in the drag path. Drag velocities over the bottom in

both commercial fishing operations and in our study are assumed to be similar. If 2.6% of the lobsters observed are retained or injured, with 50% of these lobsters killed, then the total number of lobsters estimated to be destroyed by commercial scallop fishing in 1980 was 22 lobsters. If each lobster weighed 0.5 kg and was valued at \$6.60 kg^{-1}, then the loss would be about \$73. In comparison, at \$8.27 kg^{-1} of scallop meat in May, 1980 (Jamieson et al. 1981c), the scallop landings from these two fished areas had an estimated value of \$12,483.

If lobster abundance was as high as that in the unfished area, i.e., 3.03 lobsters/1000 m^2, then 139 lobsters, with a value of \$460, would have been destroyed. In both instances, this loss is negligible in comparison to the values of the lobster and scallop fisheries. These conclusions are in agreement with the observations of Scarratt (1973) and Pringle and Sharp (1980) in their assessments of the impact of Irish moss raking on lobster populations.

ACKNOWLEDGMENTS

We thank M. Beattie, D. Duggan, S. Hamet, M. Lundy, D. R. Maynard, and N. Witherspoon for diving assistance; Captains E. Wedge and M. Ellis of chartered vessels for their help and advice; D. J. Scarratt and J. D. Pringle for their support and manuscript review, and in particular, R. Chandler, M. Etter, D. R. Maynard, and J. D. Pringle for coordinating field studies and/or assistance in data analyses.

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AGE, GROWTH, AND DISTRIBUTION OF LARVAL SPOT, *LEIOSTOMUS XANTHURUS*, OFF NORTH CAROLINA

Stanley M. Warlen and Alexander J. Chester[1]

ABSTRACT

Age and growth of the early life history stages of spot, *Leiostomus xanthurus*, were determined from daily growth increments on otoliths of larval and early juvenile spot collected from Beaufort Inlet, NC, to the continental shelf break during the fall and winter of 1978-79 and 1979-80. Spawning occurred on the mid to outer continental shelf between early November and early March, but appeared to be concentrated from mid-December through January. Generally, the youngest larvae were found further offshore; ages and lengths increased closer to shore. Larvae entered the estuary at an average age of 59 days (range 40-74 days) and an average size of 13.6 mm (range 11.3-15.6 mm). Significantly younger and smaller larvae immigrated at the beginning and end of the immigration period. Fish entered the estuary segregated by age as indicated by the small within-sample variation in age. A Gompertz growth equation was used to express the relationship between age and standard length for 69 larvae collected in 1978-79 and 557 collected in 1979-80. Spot grew from about 1.6 mm SL at hatching to 17-19 mm SL at 90 days. There were no significant differences in growth parameters between years; age-specific growth rates declined from ≅5%/day at age 10 days to <1%/day at age 90 days.

The larvae of a number of commercially important fishes that spawn on the outer continental shelf of the southeastern United States are transported shoreward to estuaries where development is completed (McHugh 1966; Chao and Musick 1977; Weinstein and Walters 1981; Warlen 1982). Although this general pattern of oceanic spawning and estuarine development has been known at least since publication of the work of Hildebrand and Cable (1930), most recent studies have considered only the estuarine phase (Chao and Musick 1977; Weinstein and Walters 1981), and virtually no quantitative data exist on age and size distribution or growth of larvae between the time of spawning and estuarine immigration.

Spot, *Leiostomus xanthurus*, spawn offshore and are widely distributed in coastal waters from the mid-Atlantic to Texas. Larvae have been reported from North Carolina to Massachusetts (Berrien et al. 1978), from the South Atlantic Bight (Fahay 1975; Powles and Stender 1976), and from the Gulf of Mexico (Fruge 1977; Govoni et al. 1983). Despite studies on egg and larval development (Fruge and Truesdale 1978; Powell and Gordy 1980), growth of juveniles (Weinstein and Walters 1981), and feeding ecology of larvae (Govoni et al. 1983) and juveniles (Chao and Musick 1977), little is known of the early growth history of spot. Our objectives were to 1) determine the estimated age and size distribution of young spot from the time of hatching in the ocean to recruitment into the estuary, 2) estimate larval growth rates, 3) estimate spawning times, and 4) determine when young spot enter the estuary.

METHODS

Sources of Data

Larvae were collected off Beaufort, NC, during 11 2-d cruises of the RV *John de Wolf II*, from December 1978 to April 1979 (grid design, stations 1-10) and from November 1979 to March 1980 (transect design, stations 11-19) (Fig. 1). At all stations, except Beaufort Inlet, samples were obtained from oblique plankton hauls (Powles and Stender 1976) collected with 60 cm diameter bongo nets (mesh sizes 333 or 505 μm) rigged with flow meters. A surface tow was made at Beaufort Inlet. Larvae were also collected with a neuston net (Hettler 1979) about 1 mi inside the mouth of the Newport River at Pivers Island (Fig. 1) seven times from mid-December 1979 to mid-April 1980. Samples were preserved in 95% ethanol (final concentration ≅75%) within 5 min of collection.

[1]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985

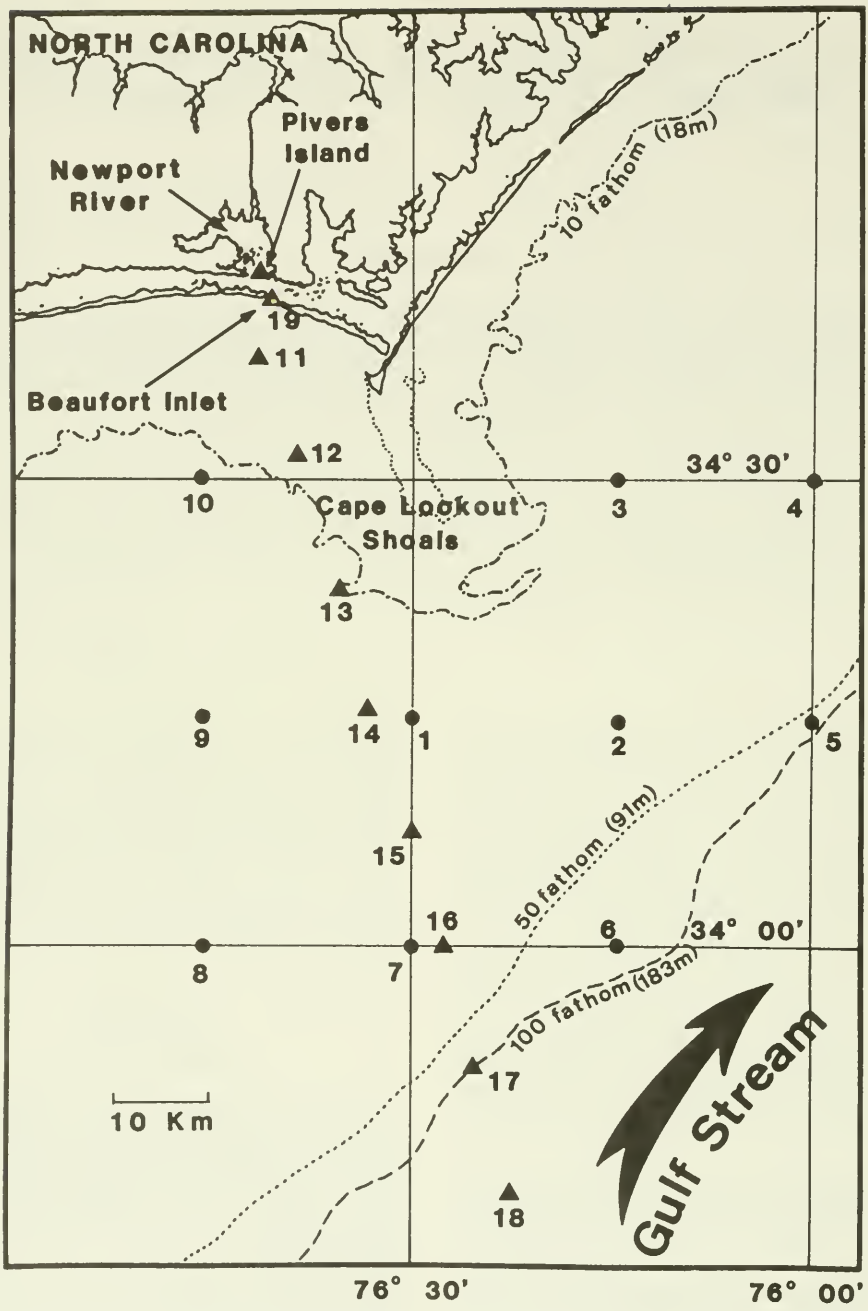

FIGURE 1.—Location of sampling sites for late-larval and early-juvenile spot in the mouth of the Newport River estuary at Pivers Island and for larval spot in the ocean off Beaufort Inlet, NC. Circles are tions sampled from December 1978 to April 1979 and triangles are those sampled October 1979 to 1980.

Estimated Age and Back-Calculated Length

We counted the number of growth increments on otoliths (e.g., Pannella 1971; Brothers et al. 1976) to estimate age (in days) of each larva. Laboratory-reared larval spot have been shown to deposit an average of 1 ring/d on their otoliths (Peters et al. 1978; Warlen 1984[2]), but do not begin to do so until 5 d after hatching, a time coincident with yolk-sac absorption and first feeding activity at 20°C (Peters et al. 1978). Therefore, we added 5 to the number of counted increments to estimate age. The spawning date of each larva was estimated by subtracting age in days from date of capture.

After we measured each larva in alcohol to the nearest 0.1 mm standard length (SL), we teased the largest pair of otoliths (sagittae) from the surrounding tissue, cleaned them in distilled water, and mounted them on a glass microslide under a thin layer of Flo-Texx[3] mounting medium. They were examined with a compound microscope fitted with a television camera. Growth increments were counted from images of otoliths on a video monitor at magnifications of at least 400×. For selected larvae, otolith radius and the growth increments along it were measured to the nearest 0.1 μm with a filar ocular micrometer. We then used Lee's (1920) modification of the direct proportion formula to back-calculate lengths and reconstruct the growth of each fish. In addition to the assumption that growth increments be daily, the reliability of back-calculated lengths requires that growth of the otolith must be linearly related to growth of the fish. We found, for larvae 2.2-12.4 mm SL, that the relation between body length and otolith radius was linear:

$$\text{body length (mm)} = 2.202 + 0.045 * \text{otolith radius } (\mu\text{m})$$
$$n = 32,\ r^2 = 0.95. \quad (1)$$

Weight-Length Relationships

Because larval fish are not weighed in many ichthyoplankton field studies, a weight-length relationship is required to describe the growth of populations, assess production in terms of dry weight, and estimate weight where only length is known. We determined a dry weight-length relationship from 125 laboratory-reared larvae and early juveniles (2.7-29.6 mm SL). Live fish were anesthetized in a solution of MS-222 (tricane methanesulfonate), removed from the solution, and measured to the nearest 0.1 mm SL. Fish were then rinsed in distilled water, placed on preweighed Nuclepore^R membrane filters, freeze-dried, and weighed to the nearest 1 μg.

RESULTS

Spawning and Larval Movement

The temporal pattern of spawning found here, though perhaps influenced by the particular dates and stations sampled (Table 1), indicated that spot is a late October-early March spawner (Fig. 2). The majority (67%) of fish collected during the fall and winter of 1979-80 were spawned during December or January (Fig. 2).

The offshore larval distribution by estimated age and length suggests that spawning occurred over the outer continental shelf. Both mean age and length varied inversely with distance from shore (Figs. 3, 4). Youngest (<25 d) and smallest (<4 mm) larvae were found most often near or in the Gulf Stream, 80-100 km off Beaufort Inlet, paralleling the 183 m depth contour (stations 5, 16, 17, 18). However, comparable ages and sizes also were found in the mid-shelf area (stations 1, 14, 15) early in the spawning season (December 1978; November and December 1979). Older (40-50 d) and larger (>8 mm) larvae generally occurred closer to shore within about 40 km of Beaufort Inlet in <25 m of water (stations 10-13, 19), except during February and March 1980 when some larvae were caught 50 km offshore at station 14. Spawning apparently is continuous between late October and late February, since young larvae occurred every month at the three offshore stations (16-18). Most spawning off North Carolina probably occurs between 75 and 95 km offshore, except for some activity in the mid-shelf area early in the spawning season. Our age-length data provided no evidence that spot spawn near shore.

Estuarine Immigration

Larvae entered the Newport River estuary over a 4-mo period from about mid-December to mid-April (Figs. 2, 5). None were caught prior to December 1979 nor after 17 April 1980. Relative abundance of larvae collected at Pivers Island dur-

[2]Warlen, S. M. 1984. Rates of increment formation in otoliths of larval gulf menhaden, *Brevoortia patronus* and spot, *Leiostomus xanthurus*. Unpubl. manuscr. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of larval spot per 100 m^3 caught off North Carolina during the seasons of 1978-79 and 1979-80. N.S. = No sample taken.

	1978-79 cruise	Station number									
No.	Date	1	2	3	4	5	6	7	8	9	10
1	6-7 Dec.	1.9	0	0	0	0	0	0	0	0	0
2	4-5 Jan.	5.0	0	N.S.	N.S.	5.6	0	0	19.3	0	0
3	31 Jan.-1 Feb.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0	0
4	7-8 Mar.	1.8	6.4	N.S.	N.S.	N.S.	0	0	1.7	2.7	0
5	26-27 Mar.	0	0	N.S.	N.S.	N.S.	0	0	0	0	13.3
6	23-24 Apr.	0	N.S.	0	0	0	0	0	0	0	0
	1979-80 cruise	Station number									
No.	Date	Inlet[1]	11	12	13	14	15	16	17	18	
7	15-16 Nov.	N.S.	0	0	0	N.S.	43.1	3.3	N.S.	N.S.	
8	3-4 Dec.	N.S.	0	0	3.1	1.1	0	4.0	1.1	45.0	
9	15-16 Jan.	N.S.	2.4	0.4	0.7	108.6	8.8	4.1	N.S.	N.S.	
10	11-13 Feb.	N.S.	0	0	4.1	31.5	17.9	0.6	0.3	2.3	
11	19-20 Mar.	65.6	0	0	0.7	4.2	11.4	0.4	0.6	0	

[1]Same as station 19.

ing the winter periods of 1967-70 showed major immigration peaks in February and March (unpublished data from R. M. Lewis, Beaufort Laboratory; Thayer et al. 1974). The duration of estuarine immigration generally reflected the duration of the spawning season (Fig. 2).

Statistically significant monthly variations (ANOVA, $P < 0.05$) in both age and length of larvae entering the Newport River estuary were observed from December to April (Fig. 5). Mean age at entry increased linearly from December to March and then decreased in April. Thus, larvae spawned at the beginning or end of the season spent relatively less time in the offshore environment than did larvae spawned in the middle of the season. Length followed a similar trend, except during January and early February when it remained about constant, indicating a declining rate of growth. As determined from seven samples collected at Pivers Island (Fig. 5) and one at Beaufort Inlet (19 March 1980), spot entering the estuary averaged 59 d-old (range 40-80).

In general, larvae entering the estuary together had similar spawning dates. As a rule, 50% of the fish in any Pivers Island sample had been spawned within a period of 5 d and all had been spawned within a period of 14 d (Fig. 2). The one exception was the last sample from Pivers Island in which several larvae were more than a month older than the majority of fish. We infer from the generally small variation in age of fish within a sample that a continuum of cohorts moved past Pivers Island enroute to the upstream parts of the estuary and that early juveniles entered the lower estuary segregated by age.

Growth Estimates

Average growth of larvae was described by the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel and Lasker 1976) fitted to estimated age and size at time of capture data for 1978-79 and 1979-80 (Fig. 6). Variance about the estimated growth curve was assumed to represent genetic differences in growth potential and the effects of differing environmental conditions over the year (Pennington 1979). To stabilize the variance of length over the observed age interval, we used the log-transformed version of the Gompertz growth equation:

$$\ln [L_{(t)}] = \ln [L_{(0)}] + \frac{A_{(0)}}{\alpha} [1 - e^{-\alpha t}] \qquad (2)$$

where $L_{(t)}$ = length at time t,
$L_{(0)}$ = length at $t = 0$,
$A_{(0)}$ = specific growth rate at $t = 0$,
α = rate of exponential decay of the specific growth rate.

The time origin ($t = 0$) was selected as hatching time (day 0) and values for $L_{(0)}$, $A_{(0)}$, and α were obtained by nonlinear regression. Age accounted for 96% of the variation in length for one year class (1978-79) and 91% of the variance in length for the other (1979-80) in the log-transformed models. We estimated that spot grew from about 1.6 mm SL at hatching to 17-19 mm at 90 d. The predicted size at hatching agrees well with laboratory observations of Powell and Gordy (1980). Population growth

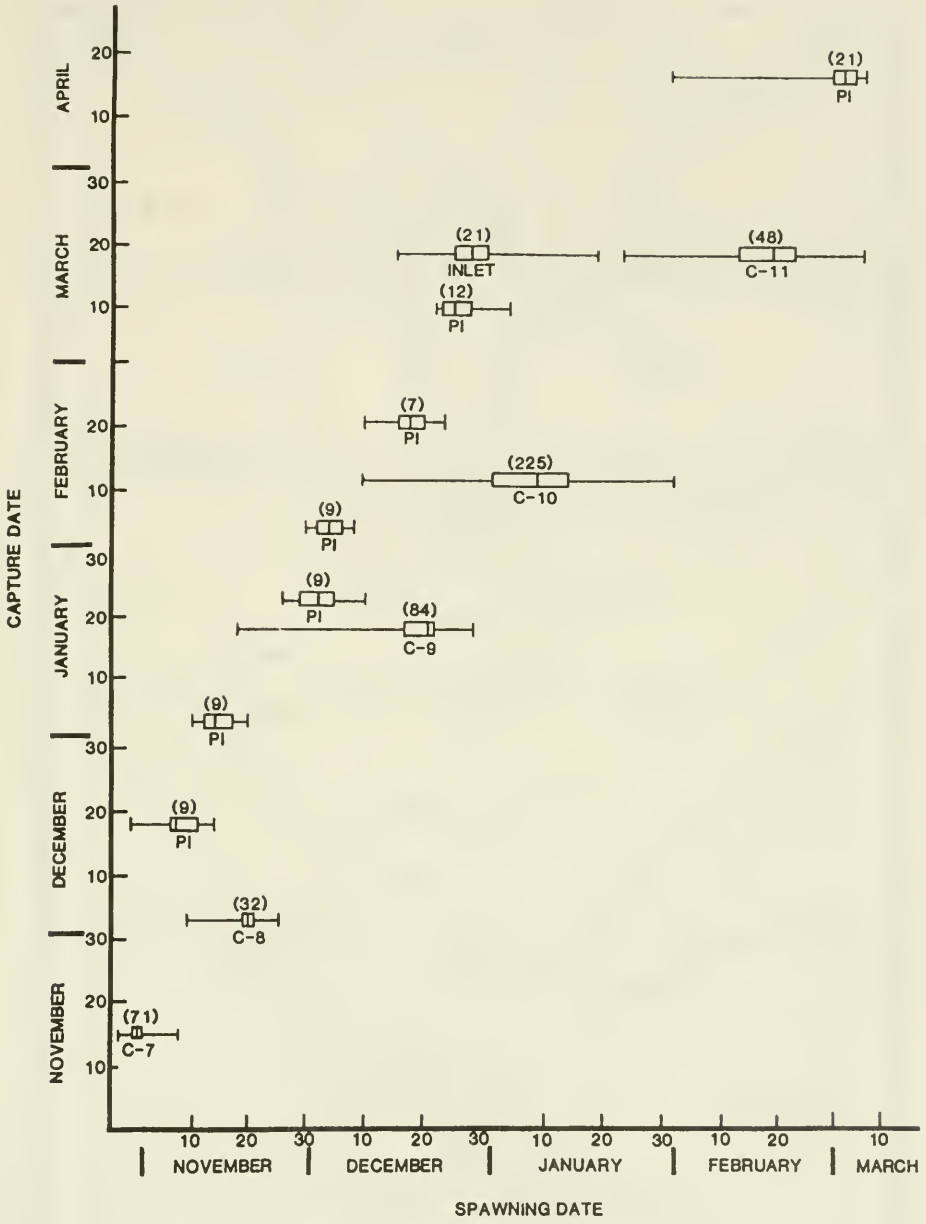

FIGURE 2.—Schematic plots of the spawning times of larval spot caught in the ocean (cruises 7-11 of RV *John de Wolf II*) and late-larvae/early-juvenile spot caught in the Newport River estuary at Pivers Island, NC. In each distribution, the vertical line is the median value and 50% of the data points fall within the block. Lines beyond the boxes represent the range of data points.

curves were not significantly different between years [Hotelling's T^2 test of $A_{(0)}$, α, and $L_{(0)}$; Bernard (1981) as modified by Hoenig and Hanumara (1983)]. Age-specific growth rates for both years declined from ≅5%/d at age 10 d to <1%/d at age 90 d.

To determine differences in growth rates for two groups of larvae of different ages but from the same cohort, we back-calculated lengths at 5-d intervals up to 25 d for 10 larvae caught at stations 15 and 16 on 15-16 January 1980 and for 10 larvae caught at Beaufort Inlet on 19 March 1980 (Table 2). Although the estimated mean spawning date for

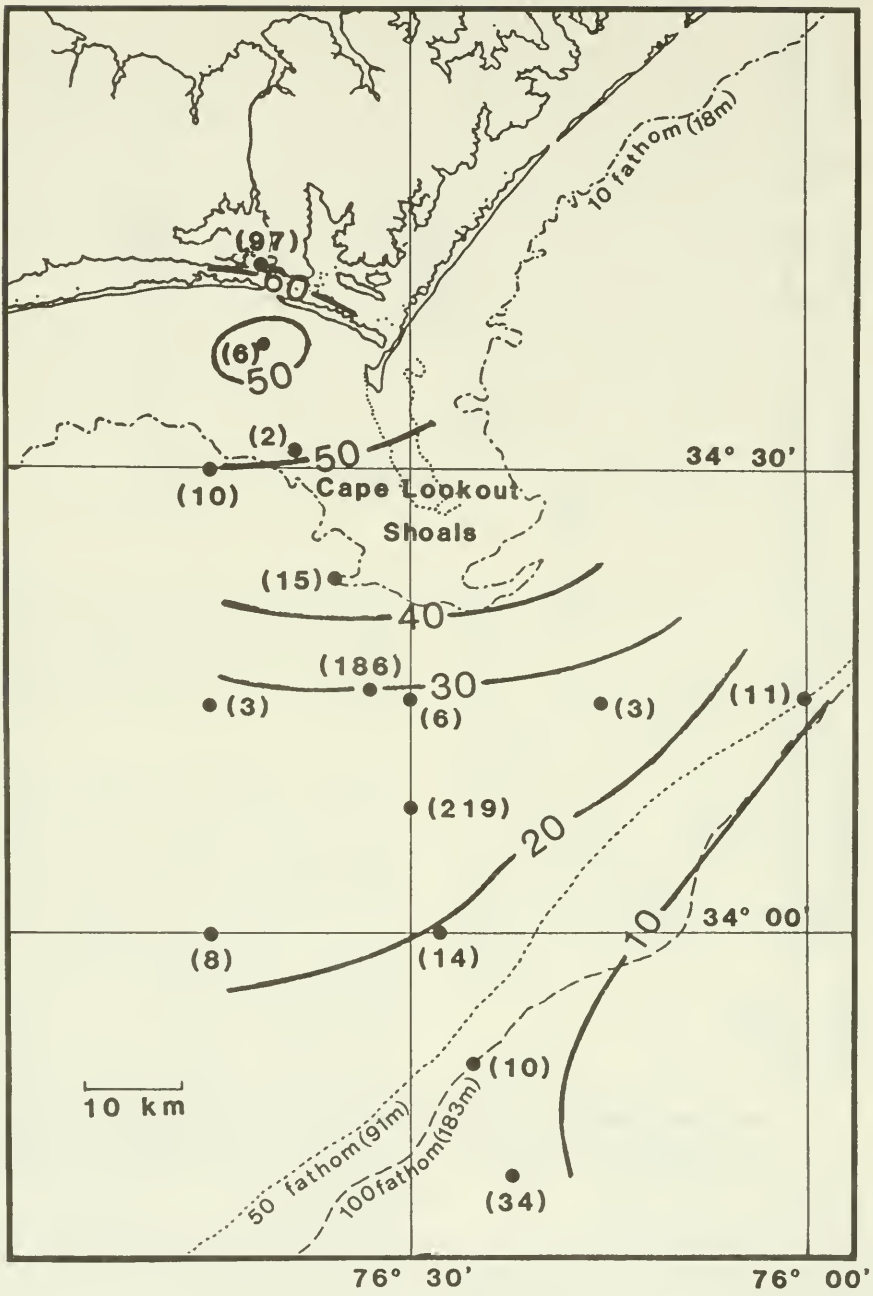

FIGURE 3.—Contour plots of the mean ages of larval spot averaged by station for all samples collected by the RV *John de Wolf II*, December 1978-April 1979 and November 1979-March 1980, and for early juveniles collected at Pivers Island, NC, October 1979-April 1980. Numerals in parentheses are the numbers of fish aged.

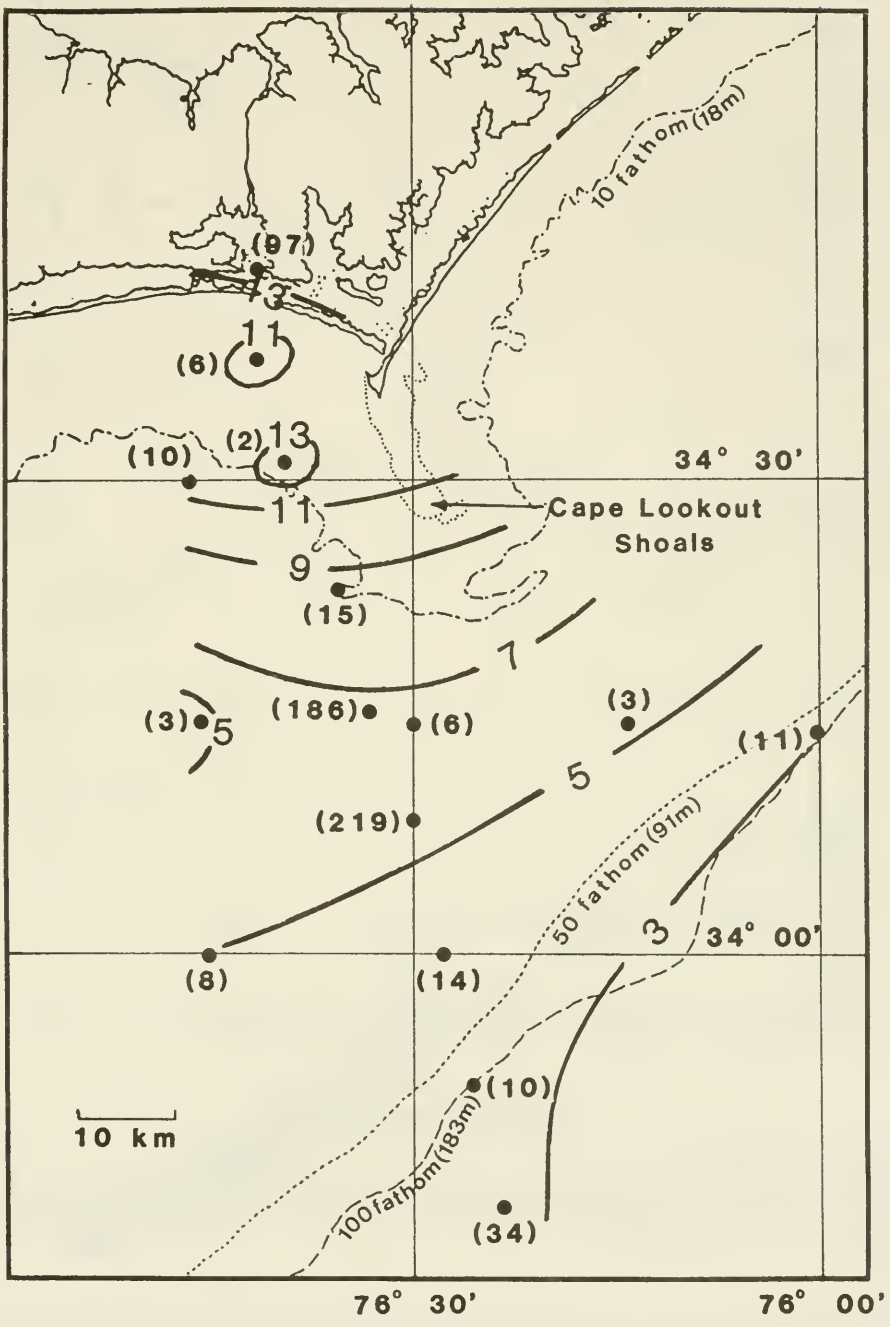

FIGURE 4.—Contour plots of the mean standard length of larval spot averaged by station for all samples collected by the RV *John de Wolf II*, December 1978-April 1979 and November 1979-March 1980, and for early juveniles collected at Pivers Island, NC, October 1979-April 1980. Numerals in parentheses are the number of fish collected and measured.

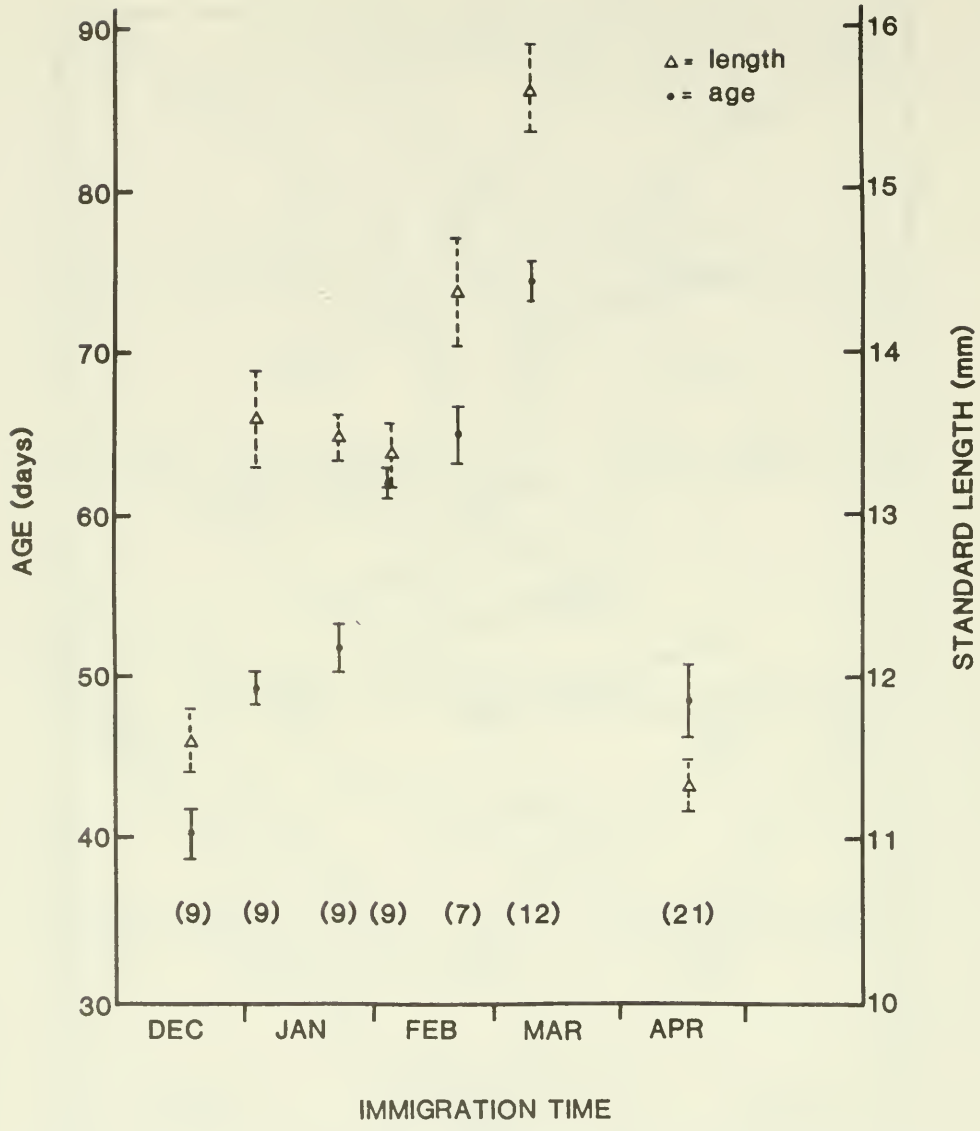

FIGURE 5.—Age (mean ±1 standard error) and standard length (mean ±1 standard error) of late-larval spot entering the Newport River estuary in North Carolina, December 1979-April 1980. The numbers of fish measured and aged at each sampling date are in parentheses.

both groups was identical (22 December 1979), the variance about the mean was greater for Inlet-caught fish. Consequently, back-calculated lengths also were more variable for Inlet-caught fish (F-test, $P < 0.05$), but on the average they appeared to be larger at every age (t-test corrected for unequal variance, $P < 0.05$).

Significant differences were found for the weight-length relation (Fig. 7) of laboratory-reared larvae ≤6 mm and those >6 mm (ANCOVA, $P < 0.001$). We selected 6 mm as the dividing point because basic changes in body form had been observed to occur at around 6 mm (Powell and Gordy 1980). The length exponent for spot ≤6 mm SL (4.201) was close to the mean value (4.152) reported by Laurence (1979) for larvae of seven marine fishes, while larvae > 6 mm (3.282) approached isometric growth (Ricker 1975).

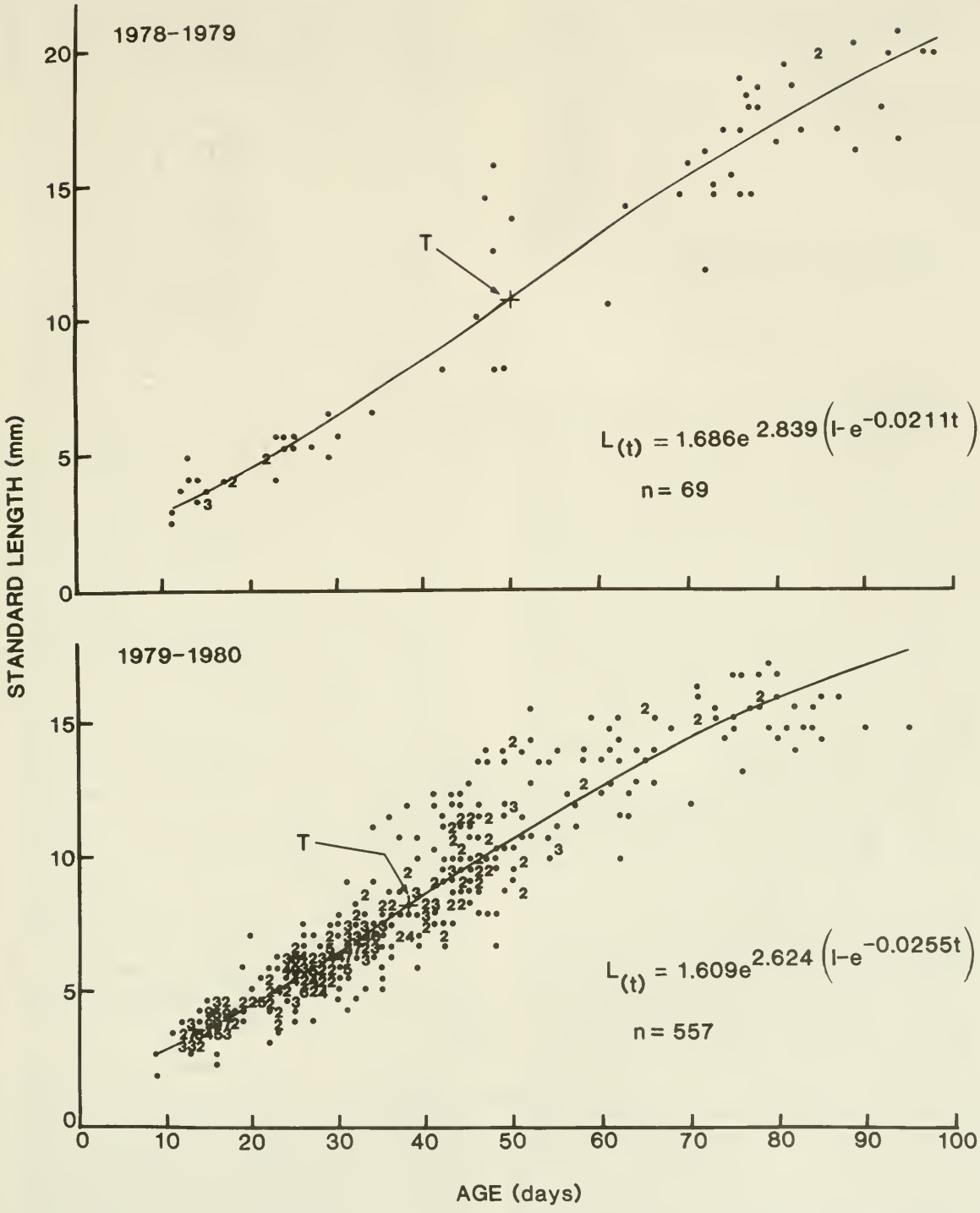

FIGURE 6.—Growth of larval and early-juvenile spot collected from oceanic and estuarine waters of North Carolina in the fall-winter, 1978-79 and 1979-80. The Laird-Gompertz growth model was used to describe the data. Estimates of the parameters were obtained by fitting the log-transformed version of the model to the data. "T" is the point of maximum absolute growth (inflection point) in the growth curve.

TABLE 2.—Mean back-calculated standard length of 10 spot from each of two collections of the same cohort (average spawning date 22 December 1979) taken about 2 mo apart in 1980.

Age (d)	15-16 January Stations 15-16[1] SL (mm)	SD	N	19 March Station 19 (Beaufort Inlet)[2] SL (mm)	SD	N
5	3.1	0.13	10	3.5	0.39	10
10	3.7	0.15	10	4.4	0.49	10
15	4.6	0.32	10	5.1	0.62	10
20	5.1	0.34	7	6.0	0.67	10
25	6.0	0.35	2	7.0	0.80	10

[1]Larval mean age, 23 d; mean size, 5.7 mm
[2]Larval mean age, 83 d; mean size, 15.0 mm

DISCUSSION

Although spot is a winter spawner, it spawns in relatively warm water. Very young larval spot (≤15 d) occurred only in water above 19.3°C, an observation corroborated by experimental evidence indicating that spot spawn only between 17.5° and 25°C (Hettler and Powell 1981). In late fall and early winter off North Carolina, such warm temperatures are found only on the outer continental shelf near the Gulf Stream. Newly ripe adults probably emigrate in the fall of the year from the cooling waters of bays and sounds in Virginia (Hildebrand and Schroeder 1928), North Carolina (Roelofs 1951), and South Carolina (Dawson 1958) to spawn in such warm waters. Hildebrand and Schroeder (1928) and Dawson (1958) also suggested that spot spawn along the outer continental shelf.

Warm coastal waters in the fall and the influence of warm Gulf Stream waters later in the season may provide a suitable spawning temperature regime over a long period. The extended (4.5 mo) spawning season of spot is typical of the general pattern for Atlantic coast sciaenids (Powles 1981). The spawning season of spot in North Carolina in 1979-80 was similar to that found by Hildebrand and Cable (1930) in North Carolina and by Dawson (1958) in South Carolina. Because most of the larvae caught off North Carolina were spawned in December and January, we conclude that these are the months of peak spawning. This conclusion is supported by the observation that peak estuarine immigration occurs in February and March (unpublished data from R. M. Lewis, Beaufort Laboratory; Thayer et al. 1974) for fish we estimate to have been about 2 mo-old. Hildebrand and Cable (1930) and Lewis and Judy (1983) also inferred, from length-frequency information, that peak spawning occurs in December and January.

The trend of decreasing larval age and size (Figs. 2, 3) with distance from shore supports the idea that spot spend virtually their entire larval period in the ocean. Berrien et al. (1978) and Lewis and Judy (1983) also noted an inverse trend of size with distance from shore in the same area to 79 km offshore. A similar trend may exist in the Gulf of Mexico where Fruge (1977) found small larval spot to be most abundant 60-80 km off the Louisiana coast. By the time larvae have been transported to shore and enter estuarine nursery areas, they have reached the late larval or early juvenile stage.

Although the mechanism is unclear by which larval spot from 74 to 93 km offshore arrive at the estuary in about 60 d, their initial onshore movement is probably a passive transport by water currents in Onslow Bay. A consistent counterclockwise eddy (Stefansson et al. 1971) and a strong indication of bottom drift in a northerly direction on the outer and mid-continental shelf and directly to the coast inshore during January-April (Bumpus 1973) could aid in the transport of larvae. Nelson et al. (1977) considered that zonal Ekman transport was a significant mechanism for movement of larval Atlantic menhaden, *Brevoortia tyrannus*, from offshore spawning grounds to inshore nursery grounds in the same study area at about the same season of year. Data from recent years, however, does not lend support for this hypothesis (Schaaf[4]). A recent analysis by Yoder (1983) suggested that mean Ekman transport does not favor onshore flow in surface waters during winter off the southeastern United States. Rather, cross-shelf transport of larval fishes may depend on highly variable, short-term meteorological events which reverse the mean surface flow. Variations in transport rates of larvae in the ocean as well as spawning at variable distances from shore may be responsible for the seasonal differences in age and length at immigration (Fig. 5). In addition, factors affecting growth, such as temperature and the distribution of food organisms, interact with the physical factors of transport to produce the temporal pattern of age and length observed in a given year.

Young spot undergo several environmentally related changes in growth during their larval and juvenile stages. Growth in length of larval spot is rapid (initially approaching 7%/d) and coincides with the winter peak of plankton productivity in the relatively warm water of the outer continental shelf (Turner et al. 1979; Turner 1981; Yoder et al. 1981;

[4]W. E. Schaaf, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722, pers. commun. January 1984.

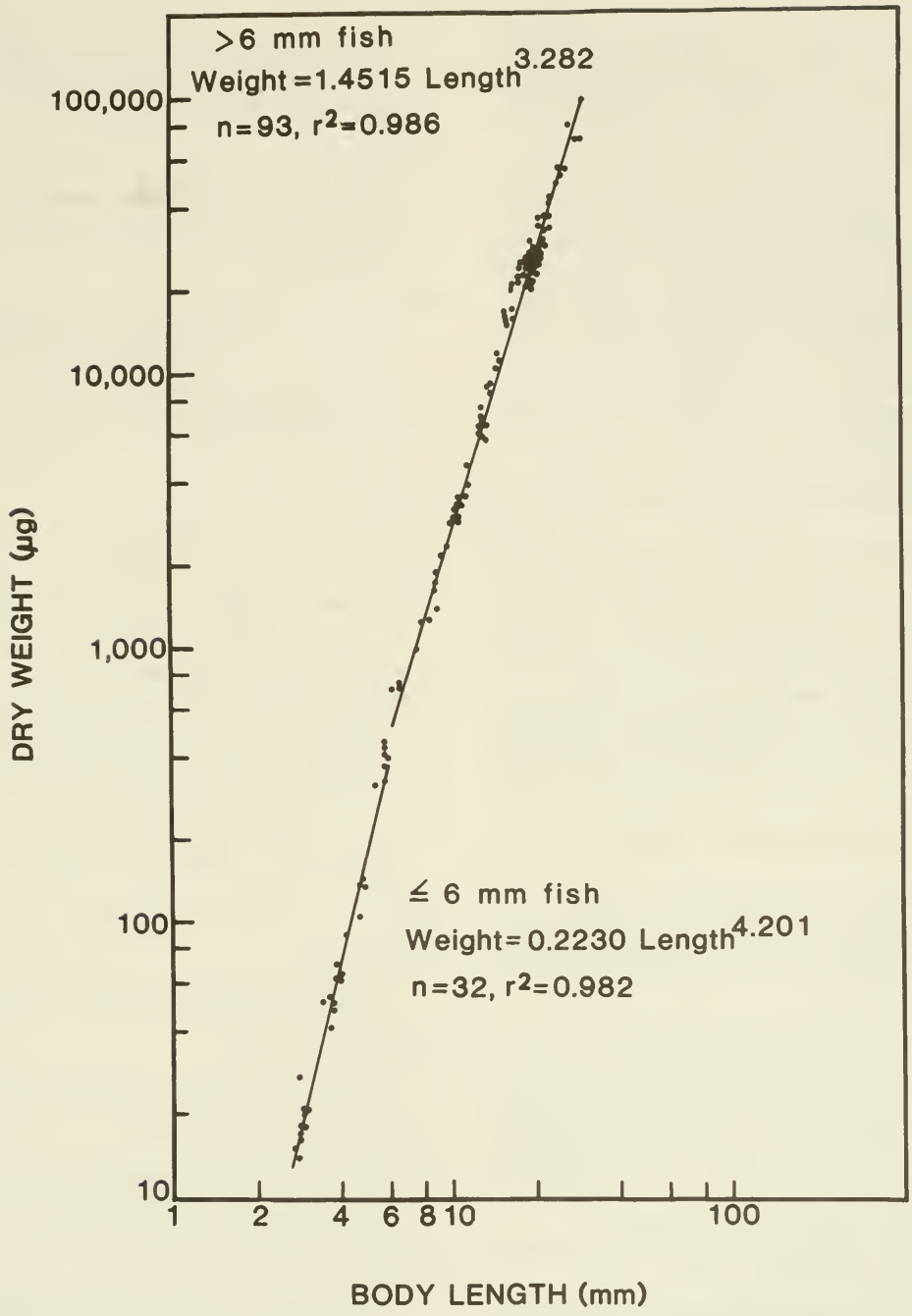

FIGURE 7.—Relationships between dry weight and standard length of spot for length classes ≤6 mm and >6 mm. Fish were from laboratory spawned and reared stocks.

Yoder et al. 1983). By the time larvae enter the cooler (often <10°C) coastal and estuarine waters, growth rate has slowed considerably (<1.5%/d). The asymptote of 22.2 mm SL (Fig. 6, 1979-80 data) estimated by our growth model corresponds closely to the size of juvenile spot collected early in their estuarine residency (Weinstein and Walters 1981). Increase in length of newly immigrated spot is relatively slow (≅0.5%/d from December to March, estimated from figure 3 of Weinstein and Walters 1981), and it is

not until after the usual peak in plankton abundance (Thayer et al. 1974) and increases in water temperature that growth rates accelerate and persist at a high level through the summer (≅1.0%/d from April to August, estimated from figure 3 of Weinstein and Walters 1981).

Within the same cohort, older fish had statistically larger back-calculated sizes at each age than did younger fish (Table 2). One explanation is that size-selective mortality (e.g., predation, Bailey 1984) favors survival of faster growing larvae and that the apparent growth rate depends on the size (and age) of larvae on which it is calculated. Alternatively, the two groups may have been spawned in different locations and experienced different environmental conditions that could affect growth.

ACKNOWLEDGMENTS

We thank Mary Boyd for preparing and reading the otoliths and John Merriner, William Nicholson, and William Schaaf for their critical reviews of earlier drafts of this manuscript. We also thank the many participants on the 11 cruises of the RV *John de Wolf II*. This research was supported by a cooperative agreement between the National Marine Fisheries Service, NOAA, and the U.S. Department of Energy.

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DIET OF PACIFIC COD, *GADUS MACROCEPHALUS*, AND PREDATION ON THE NORTHERN PINK SHRIMP, *PANDALUS BOREALIS*, IN PAVLOF BAY, ALASKA

W. D. Albers and P. J. Anderson[1]

ABSTRACT

Analysis of 455 Pacific cod, *Gadus macrocephalus*, stomachs collected in 1980 and 1981 from Pavlof Bay, in the western Gulf of Alaska, showed considerable predation on northern pink shimp, *Pandalus borealis*. The most frequently occurring prey items were pink shrimp, *P. borealis*, 63%; euphausids, 41%; walleye pollock, *Theragra chalcogramma*, 27%; and capelin, *Mallotus villosus*, 26%. Pandalid shrimp and snow (Tanner) crab occurred more frequently with increasing cod size (30-69 cm fork length). Euphausids decreased in frequency of occurrence with increasing cod size. Pink shrimp length distributions from cod stomachs and trawl samples were similar. Estimated consumption of pink shrimp by cod in Pavlof Bay ranged from 142 to 857 t over a 112-day period from late May through mid-September 1981. Cod predation may be one reason for the failure of the pink shrimp stock to rebuild in Pavlof Bay following closure of the commercial fishery in 1979. Cod predation may also play a role in keeping other reduced pink shrimp stocks in the western Gulf of Alaska from rebuilding to former levels.

Pacific cod, *Gadus macrocephalus*, predation on northern pink shrimp, *Pandalus borealis*, in Pavlof Bay (Fig. 1) was studied to determine if it is a factor in keeping the pink shrimp stock from rebuilding there. National Marine Fisheries Service (NMFS) and Alaska Department of Fish and Game (ADF&G) survey data from the late 1970's indicate that when pink shrimp populations in regions of western Alaska began to decrease, cod abundance started to increase. Pink shrimp has been reported to be an important food item in the diet of Pacific cod in the Gulf of Alaska (Jewett 1978; Hunter 1979). Predation of pink shrimp by cod may have substantial influence on shrimp stock abundance.

Pavlof Bay was chosen as the study area because it supported a commercial fishery for pandalid shrimp in the 1970's and is suspected to contain a geographically isolated stock of pink shrimp (Anderson 1981). From 1972 through 1979, 13,641 t of pink shrimp were commercially harvested from Pavlof Bay (calculated from ADF&G commercial catch data and NMFS survey data). Survey data from Pavlof Bay indicate that in 1977 and 1978 when pink shrimp abundance began decreasing, cod abundance began increasing (Fig. 2). Following the 1979 season the bay was closed to commercial shrimping due to depressed shrimp abundance levels which remained low through 1983.

This report presents data which suggest that Pacific cod predation is a factor in keeping shrimp stocks from rebuilding. The summer diet of cod, prey size selectivity, and an estimate of pink shrimp biomass consumed by cod in Pavlof Bay during a 112-d period from late May through mid-September 1981 are discussed.

MATERIALS AND METHODS

Pacific cod were collected from 31 tows during three trawl surveys. The first collection was done by NMFS on 25-26 August 1980, the second by ADF&G on 23-25 May 1981, and the third by NMFS on 10-11 September 1981. The collecting was done during daylight hours over a period of about 14 h a day. All three surveys used a high-opening shrimp trawl with an 18.6 m headrope and footrope described by Wathne (1977). Mesh size of the trawl is 32 mm and path-width is about 10 m. Each tow was about 1.8 km in length. Randomly selected sampling locations were restricted to depths >55 m since previous surveys showed that neither shrimp nor cod were found in abundance in shallow water. Both shrimp and cod are uniformly distributed at depths >55 m in Pavlof Bay.

When possible, five stomachs per 5 cm interval of fork length (FL) were removed from every trawl catch and preserved in 10% Formalin[2]. In the

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

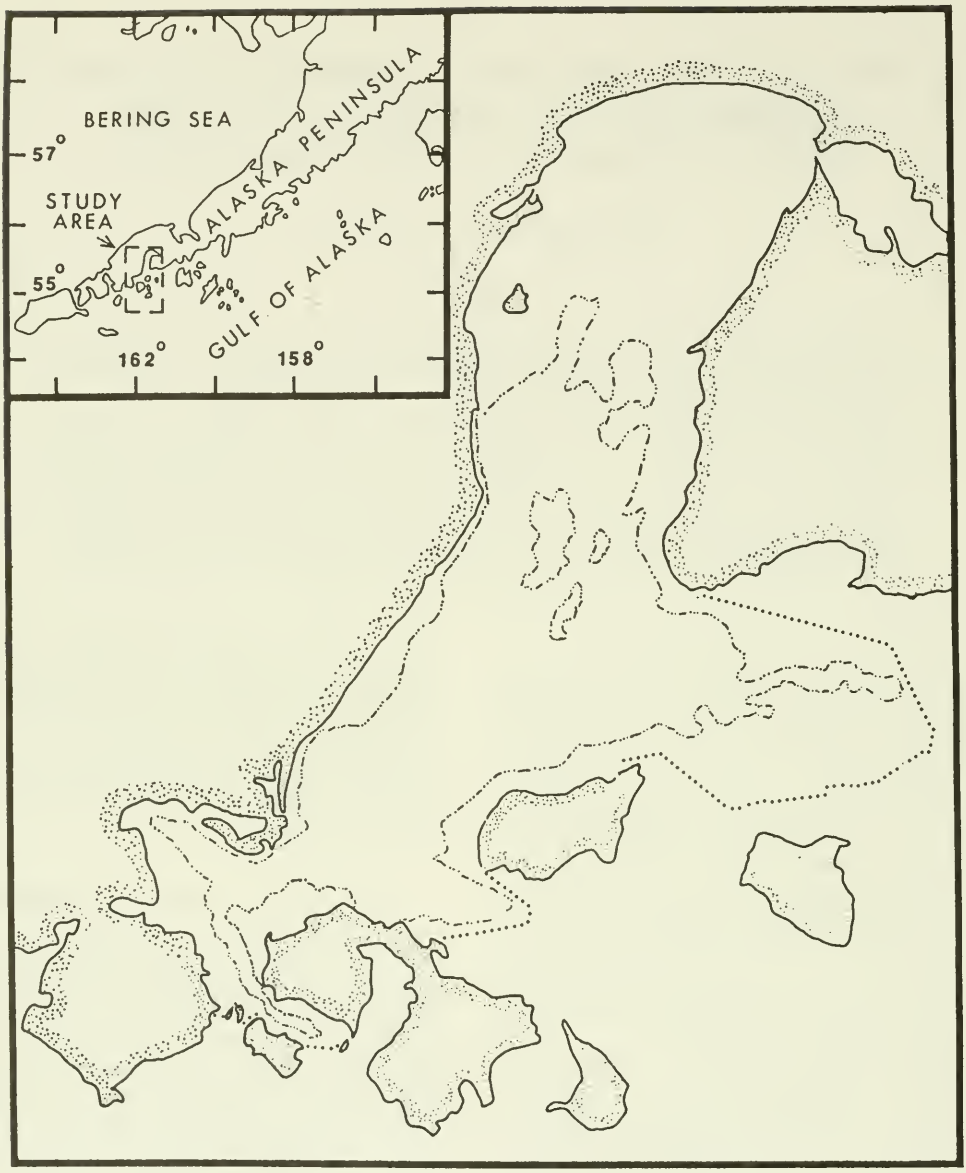


FIGURE 1.—Location of the study area of pink shrimp and Pacific cod (55 m isobath indicated by dotted/dash-line).

laboratory, prey items were sorted to the lowest possible taxon. Frequency of occurrence (number of stomachs containing the food item), number of each prey item, volume by water displacement (nearest 0.1 mL), and wet weight (nearest gram) were recorded. From these measurements, percentages by frequency of occurrence, number, and volume were calculated from non-empty stomachs only.

Size composition was recorded for prey species of commercial importance including pink shrimp (carapace length, CL); humpy shrimp, *Pandalus goniurus*, CL; snow (Tanner) crab, *Chionoecetes bairdi*, carapace width (CW); and walleye pollock, *Theragra chalcogramma*, fork length (FL). Additionally, size composition was recorded for samples of pink shrimp (CL), humpy shrimp (CL), Pacific cod (FL), and walleye pollock (FL) caught in each tow.

To determine if Pacific cod were feeding on selected sizes of pink shrimp, the Kolmogorov-Smirnov test (Sokal and Rohlf 1969) was used to test

for a significant difference between pink shrimp length distributions measured from Pacific cod stomachs and those measured from the trawl. Pink shrimp lengths tested were ≥16.5 mm CL. Anderson (1981) reported that shrimp <16.5 mm CL are not fully vulnerable to trawl capture.

Population biomass estimates for pink shrimp and Pacific cod were calculated using the area swept technique (Alverson and Pereyra 1969).

An estimate of pink shrimp biomass consumed by Pacific cod in Pavlof Bay during the 112-d period between the late May and mid-September 1981 surveys was determined through methods described by Minet and Perodou (1978). Undigested weights (W) of pink shrimp were determined from carapace lengths using the weight-length relationship $W = 0.000802\ (CL)^{2.903}$ (calculated from Pavlof Bay pink shrimp length-weight data). The mean weight of pink shrimp per stomach for each 5 cm length group of Pacific cod was calculated from stomachs where at least 80% of the pink shrimp were measurable (Table 1). A stomach which contained <80% measurable pink shrimp was deemed not suitable for determining the weight of undigested shrimp consumed. These data were then weighted using 768 cod lengths measured during the three surveys. The mean weight of pink shrimp in the stomach of an average-sized cod was then estimated for each survey (Table 1).

The average rates of elimination (r) of food from Pacific cod stomachs collected during the May and September 1981 surveys were calculated from Jones' (1974) equation for food elimination rates from Atlantic gadoids including Atlantic cod, *Gadus morhua*. Jones found that the rates of elimination for the three species of gadoids studied were effectively the same, adjusting for fish and meal size, and temperature. Since Pacific cod are very similar to Atlantic cod, we used Jones' equation in the absence of more relevant information:

$$r\ (\text{g/h}) = \frac{10^{0.035\ (To\ -\ Tc)}\ X^{0.46}\ QL^{1.4}}{175}$$

where Tc = 6°C; temperature of the experiment (Jones 1974).

To = 5°C (May), 7°C (September); observed temperature in Pavlof Bay from expendable bathythermograph data.

X = 98.9 g (May), 109.0 g (September); the average weight of food found in one stomach. The average weight of food was estimated for each 5 cm length group of Pacific cod and then weighted using 502 cod lengths measured during the May and September surveys. Stomachs containing at least 60% of the greatest weight of food encountered for each cod length group were used to determine X.

Q = 0.12; the average rate of elimination of 1 g of food from the stomach of a 40 cm gadoid (Jones 1974).

L = 52.7 cm (May), 53.0 cm (September); the average length of Pacific cod calculated from 236 fish measured in May and 266 fish measured in September.

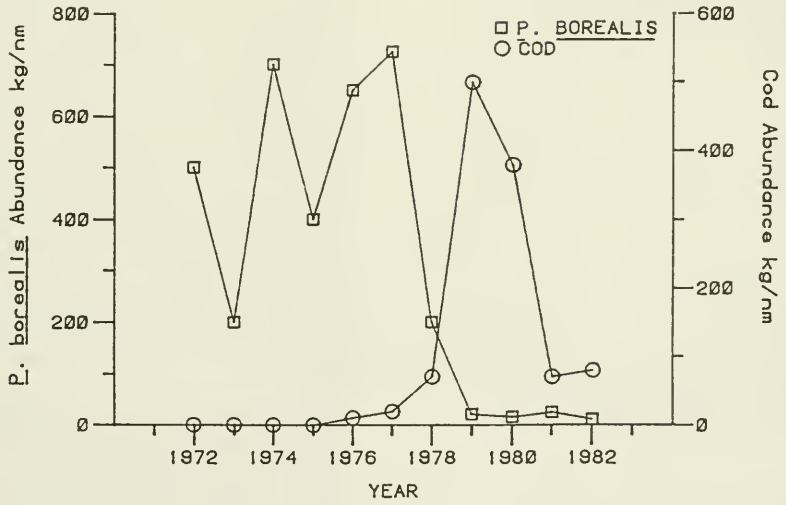


FIGURE 2.—Abundance of pink shrimp and Pacific cod from NMFS summer trawl survey data collected in Pavlof Bay, 1972-82.

TABLE 1.—Calculation of the mean weight of undigested pink shrimp in one stomach for August 1980, May and September 1981.

Length groups of cod (cm)	August 1980			May 1981			September 1981		
	A Number of cod	B Mean weight of undigested pink shrimp (g)	A×B Total weight of undigested pink shrimp (g)	A Number of cod	B Mean weight of undigested pink shrimp (g)	A×B Total weight of undigested pink shrimp (g)	A Number of cod	B Mean weight of undigested pink shrimp (g)	A×B Total weight of undigested pink shrimp (g)
30-34	2	0	0	—	—	—	—	—	—
35-39	12	0.2	2.4	2	13.6	27.2	3	2.0	6.0
40-44	49	3.5	171.5	9	9.8	88.2	14	3.0	42.0
45-49	137	3.8	520.6	44	19.3	849.2	34	10.1	343.4
50-54	56	7.7	431.2	98	27.2	2,665.6	112	11.3	1,265.6
55-59	9	8.1	72.9	66	17.8	1,174.8	81	12.9	1,044.9
60-64	1	2.5	2.5	14	57.3	802.2	22	12.7	279.4
65-69	—	—	—	3	50.8	152.4	—	—	—
Totals	266		1,201.1	236		5,759.6	266		2,981.3
Mean weight of undigested pink shrimp		$\frac{1,201.1}{266}$ = 4.5 g			$\frac{5,759.6}{236}$ = 24.4 g			$\frac{2,981.3}{266}$ = 11.2 g	

RESULTS

Cod Diet

Of 455 Pacific cod stomachs examined, 435 contained food. Data obtained from cod stomachs collected in August 1980, May 1981, and September 1981 are presented in Table 2. Combining these data, the most frequently occurring prey items were pink shrimp (63%), euphausids (41%), walleye pollock (27%), and capelin, *Mallotus villosus*, (26%). Crustaceans, mostly shrimp, crab, and euphausids, were present in 93% of the stomachs containing food and comprised 45% of the volume. Teleosts, mostly walleye pollock and capelin, were present in 60% of the stomachs containing food and comprised 54% of the volume. Gastropods, bivalves, sipunculids, and ascidians together comprised 1% of the volume.

Crustaceans made up the greatest part of the diet in the May sample and teleosts comprised the greatest part of the diet in the August and September samples (Table 2). Shrimp, mostly pink shrimp, made up 67% of the volume in May compared with 28%, combining August and September data. Crabs, mainly snow crab, comprised 10% of the volume in May compared with 3% in August-September. Teleosts, primarily walleye pollock and capelin, made up 4% of the volume in May and 65% in August-September.

Data on the 10 most frequently occurring food items was categorized by 10 cm length (FL) groups of Pacific cod in a size range of 30 through 69 cm (Table 3). Hurtubia's (1973) trophic diversity method was used to assure that enough stomach samples had been analyzed to give representative values for each length group. Pink shrimp occurred most frequently in all but one length group (30-39 cm) and was the dominant food item by volume in all length groups. Pink shrimp and snow crab increased both in frequency of occurrence and volume with increasing cod size. Conversely, euphausids were the most frequently encountered food item in the 30-39 cm length group, but their frequency of occurrence and volume decreased with increasing cod size. No trends were evident for the occurrence of teleosts. Although data from the three surveys were combined for Table 3, the above trends were evident in each of the surveys.

The size ranges and mean sizes of pink shrimp and humpy shrimp consumed by Pacific cod were similar in general to those found in the trawl (Table 4). Size range and mean size of walleye pollock consumed by cod were considerably smaller than those fish captured by the trawl.

TABLE 2.—Percent frequency of occurrence (*F*), percent by number (*N*), and percent by volume (*V*) of food items in Pacific cod stomachs for August 1980 and May and September 1981. Food categories followed by (total) is the sum of the food items that fall within that category for percent number and percent volume. Percent frequency of occurrence is the number of stomachs containing the food category or item divided by the total number of stomachs containing food.

Food items	August 1980 (*n* = 202)			May 1981 (*n* = 63)			September 1981 (*n* = 170)		
	F	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Crustacea (total)	93.1	92.2	29.4	100.0	99.5	95.0	91.2	57.6	37.6
Amphipoda	—	—	—	—	—	—	1.8	0.3	<0.1
Euphausiacea	53.5	77.0	6.1	81.0	87.3	17.8	12.4	3.3	0.1
Decapoda									
Natantia (total)	71.3	15.0	23.0	76.2	10.4	67.1	80.6	46.1	32.2
Pandalidae	—	—	—	3.2	0.1	0.1	1.8	0.2	<0.1
Pandalus borealis	56.9	9.3	18.5	65.1	7.6	59.7	70.6	34.9	29.9
Pandalopsis dispar	—	—	—	17.5	0.5	1.0	1.2	0.1	<0.1
Pandalus goniurus	20.3	1.7	2.3	25.4	0.4	1.7	4.1	0.9	0.5
Pandalus hypsinotus	0.5	<0.1	0.1	4.8	0.1	1.1	1.2	0.1	0.3
Crangonidae	—	—	—	—	—	—	4.1	0.8	0.2
Crangon sp.	3.0	0.2	0.1	7.9	0.1	0.2	2.9	0.5	<0.1
Crangon communis	2.5	0.2	0.1	12.7	0.2	0.3	18.2	2.9	0.5
Crangon dalli	—	—	—	—	—	—	3.5	0.5	0.1
Argis sp.	—	—	—	4.8	0.1	0.3	1.2	0.1	<0.1
Argis dentata	—	—	—	4.8	0.1	0.3	1.8	0.2	<0.1
Argis lar	—	—	—	—	—	—	4.7	0.7	0.2
Hippolytidae	0.5	<0.1	<0.1	6.3	0.1	0.1	—	—	—
Eualus sp.	0.5	<0.1	<0.1	—	—	—	—	—	—
Eualus macilenta	—	—	—	11.1	0.3	0.2	5.3	0.8	<0.1
Eualus suckleyi	0.5	<0.1	<0.1	1.6	0.1	0.2	2.9	0.4	0.1
Unidentified Natantia	26.7	3.6	1.9	30.2	0.7	1.9	20.0	3.0	0.4
Reptantia (total)	3.5	0.2	0.3	39.7	1.8	10.1	31.2	7.9	5.3
Lithodidae									
Paralithodes camtschatica	0.5	<0.1	<0.1	—	—	—	—	—	—
Majidae									
Chionoecetes bairdi	1.5	0.1	0.2	41.2	1.8	10.0	25.3	6.2	4.7
Paguridae	2.0	0.1	0.1	—	—	—	0.6	0.1	<0.1
Pagurus aleuticus	—	—	—	—	—	—	0.6	0.1	0.2
Pinnotheridae									
Pinnixa sp.	—	—	—	1.6	<0.1	0.1	8.2	1.5	0.4
Osteichthyes (total)	59.4	8.1	68.8	15.9	0.4	3.7	77.1	38.2	60.6
Ammodytes hexapterus	1.5	0.1	0.1	1.6	<0.1	<0.1	—	—	—
Gadus macrocephalus	—	—	—	—	—	—	1.2	0.1	1.8
Hippoglossoides elassodon	0.5	<0.1	1.3	—	—	—	4.7	0.7	4.1
Icelus sp.	—	—	—	—	—	—	0.6	0.1	0.3
Lumpenella longirostris	—	—	—	1.6	<0.1	0.1	—	—	—
Lumpenus sp.	—	—	—	1.6	<0.1	0.1	10.0	1.8	1.3
Lumpenus fabricii	—	—	—	—	—	—	0.6	0.1	<0.1
Lumpenus maculatus	0.5	<0.1	<0.1	—	—	—	—	—	—
Lumpenus sagitta	—	—	—	1.6	<0.1	0.1	—	—	—
Lycodes sp.	—	—	—	—	—	—	0.6	0.1	0.6
Lycodes brevipes	—	—	—	—	—	—	1.2	0.1	0.9
Mallotus villosus	28.7	4.6	32.7	4.8	0.1	1.4	29.4	8.9	20.5
Theragra chalcogramma	13.4	.7	24.8	1.6	<0.1	1.2	51.8	17.0	21.9
Trichodon trichodon	—	—	—	—	—	—	5.9	0.7	4.3
Zaprora silenus	—	—	—	—	—	—	0.6	0.1	0.7
Unidentified Osteichthyes	30.7	2.7	9.9	14.3	0.3	0.8	37.1	8.5	4.2
Bivalvia (total)	1.0	0.1	0.1	4.8	0.1	0.1	14.7	3.1	0.1
Clinocardium sp.	0.5	<0.1	<0.1	3.2	<0.1	<0.1	1.8	0.2	<0.1
Macoma sp.	—	—	—	—	—	—	0.6	0.1	<0.1
Yoldia sp.	—	—	—	3.2	<0.1	<0.1	12.4	2.6	<0.1
Unidentified Bivalvia	0.5	<0.1	<0.1	1.6	<0.1	<0.1	1.8	0.2	<0.1
Gastropoda (total)	1.0	0.1	0.1	3.2	0.1	0.1	0.6	0.1	<0.1
Naticidae	1.5	0.1	0.1	1.6	<0.1	<0.1	—	—	—
Neptunidae	—	—	—	1.6	<0.1	<0.1	0.6	0.1	<0.1
Trochidae									
Margarities sp.	—	—	—	1.6	<0.1	<0.1	—	—	—
Unidentified Gastropoda	—	—	—	1.6	<0.1	<0.1	—	—	—
Ascidiacea	0.5	<0.1	0.2	—	—	—	—	—	—
Sipuncula (Phylum)	0.1	<0.1	0.1	1.6	<0.1	0.1	2.4	0.4	0.6
Plant	2.0	0.1	1.4	3.2	<0.1	0.9	4.7	0.6	1.0
Pebbles	2.5	—	0.1	19.0	—	0.4	18.8	—	0.4

TABLE 3.—The 10 most frequently occurring food items are categorized by 10 cm length (FL) groups of Pacific cod from 30 to 69 cm. Data is presented by percent frequency of occurrence (*F*), percent by number (*N*), and percent by volume (*V*).

	30-39 cm (*n* = 20)			40-49 cm (*n* = 216)			50-59 cm (*n* = 173)			60-69 cm (*n* = 23)		
Food items	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Euphausiacea	78.8	51.3	7.5	54.7	58.3	9.0	48.1	54.8	8.9	27.3	32.7	3.0
Pandalus borealis	36.4	15.1	31.9	61.0	19.0	30.6	69.9	17.7	36.4	81.8	29.7	47.6
Pandalus goniurus	3.0	0.5	0.9	13.8	0.7	1.2	20.2	1.3	1.2	22.8	0.6	0.9
Crangon sp.	5.6	2.4	<0.1	3.5	0.2	0.1	4.0	0.3	0.1	9.0	0.3	0.2
Crangon communis	—	—	—	10.1	0.9	0.4	12.9	1.2	0.3	18.2	1.4	0.5
Eualus macilenta	11.1	0.3	0.3	5.2	0.3	0.1	6.7	0.4	0.1	—	—	—
Chionoecetes bairdi	—	—	—	11.5	1.4	2.5	26.7	3.0	5.1	59.1	5.3	9.0
Lumpenus sp.	—	—	—	4.3	0.9	0.8	3.5	0.5	0.4	4.5	0.2	0.3
Mallotus villosus	14.1	8.7	28.3	19.6	3.5	18.3	24.4	4.7	17.5	22.8	4.7	9.3
Theragra chalcogramma	16.7	9.5	8.5	20.5	4.4	15.2	22.7	6.3	16.7	13.7	6.3	3.9

All sizes of cod examined were feeding on both small and large pink shrimp. Pink shrimp length (CL) distributions measured from cod stomachs and from trawl samples began to overlap at about 12 mm (Fig. 3). Results from the Kolmogorov-Smirnov test comparing pink shrimp length distributions ≥16.5 mm CL from cod stomachs and trawl samples showed no significant difference ($P > 0.10$) in August 1980 and May 1981. There was a significant difference ($P = 0.009$) in the September 1981 sample. No significant difference between length distributions indicates that cod were not feeding on selective sizes of pink shrimp. A significant difference indicates that cod consumed a greater proportion of smaller shrimp than was captured by the trawl.

stomach were 24.4 g for May and 11.2 g for September 1981 (Table 1). Per day, the average amount of pink shrimp consumed by one cod was 8.1 g and 3.7 g for May and September, respectively. The estimated weight of an average length cod was 1,689.5 g for the May survey and 1,720.1 g for the September survey ($W = 0.00000593L^{3.168}$; Owen and Blackburn 1983). Cod biomass estimates were 1,621 t for May and 591 t September, respectively.

Based on the above parameters, estimates of pink shrimp biomass consumed were calculated using the May and September data (Table 5). With May data, Pacific cod consumed an estimated 875 t of pink shrimp over the 112-d period, whereas the

TABLE 4.—Size range and mean size of prey and trawl caught animals. Size data were not collected for snow crab in the trawl. CL = carapace length; FL = fork length; CW = carapace width.

	Number measured		Size range		Mean size	
	Prey	Trawl	Prey	Trawl	Prey	Trawl
Pink shrimp	1,143	7,823	6.5-26.0 mm (CL)	10.0-26.0 mm (CL)	16.2 mm	18.0 mm
Humpy shrimp	102	202	8.0-17.5 mm (CL)	10.5-18.5 mm (CL)	13.5 mm	13.9 mm
Walleye pollock	236	2,100	6.0-25.0 cm (FL)	6.0-63.0 cm (FL)	10.3 cm	22.8 cm
Snow crab	69	—	6.0-42.0 mm (CW)	—	22.2 mm	—

Estimate of Pink Shrimp Biomass Consumed

The extent of the Pacific cod predation on pink shrimp in Pavlof Bay was examined by estimating total biomass consumed during a 112-d period from late May through mid-September 1981. Analysis using Jones' (1974) equation indicated that for both 1981 surveys the average amount of food found in a cod stomach was digested in about 3 d. The average weights of undigested pink shrimp found in a cod

TABLE 5.—Calculation of the total pink shrimp biomass consumed by Pacific cod during a 112-d period from late May through mid-September 1981. Two estimates are presented using the May and September data.

	May 1981	Sept. 1981
Mean weight of pink shrimp consumed daily by one cod (g)	8.1	3.7
112-d consumption by one cod (g)	907.2	414.4
Weight of an average length cod (g)	1,689.5	1,720.1
Proportion of pink shrimp eaten relative to cod weight	0.54	0.24
Cod biomass estimate (t)	1,621	591
Pink shrimp biomass consumed (t)	875	142

September information suggests that cod consumed an estimated 142 t of pink shrimp over the same period.

DISCUSSION

Cod Diet

Pink shrimp was the dominant food item identified by frequency of occurrence (63%) and percent volume (31%). In the Gulf of Alaska near Kodiak Island, Jewett (1978) reported pink shrimp occurring in 4% of the Pacific cod examined, and Hunter (1979) found pink shrimp occurring in 24% of the cod, representing 16% of the diet by weight. Hunter also identified pink shrimp as the dominant food item in his study. However, our study exhibited a higher percent frequency of occurrence for that species. Unlike our study, Jewett and Hunter's studies included examinations of cod from offshore areas, which were not regions of high pink shrimp density (Gaffney 1977[3]).

The prey size ranges of walleye pollock and snow crab in our study were similar to those found by Hunter (1979). In our study, the maximum length of walleye pollock consumed by cod was 25 cm FL, although the majority were between 6 and 20 cm. Hunter (1979) reported that cod around Kodiak Island were feeding on groundfish (including walleye pollock) between 2 and 24 cm. The snow crab consumed by cod in Pavlof Bay ranged from 5 to 45 mm CW, which is similar to the size range of snow crab (1-40 mm) found in cod stomachs by Hunter (1979). Jewett (1978) reported a greater size range of snow crab occurring in cod stomachs (from 1.8 to 70 mm), yet 78% were between 7 and 23 mm. The maximum size of cod examined by Jewett was 92 cm TL (total length) compared with 69 cm FL in our study, and this difference probably accounts for his observation of larger snow crab.

We believe that cod were not feeding on selected sizes of shrimp. The size ranges and mean sizes of pink shrimp and humpy shrimp consumed by cod were similar to those found in the trawl (Table 4). However, cod did consume small (<10.0 mm CL) pink shrimp that were not captured by the trawl. We believe this is due to trawl bias toward larger shrimp. No significant difference was found between pink shrimp length distributions from cod stomachs and trawl samples in two of the three surveys, indicating that cod were not feeding on selected sizes of shrimp. There was a significant difference ($P = 0.009$) for the September 1981 survey. In this sample either cod selected slightly for smaller shrimp or the trawl caught slightly larger shrimp.

Estimate of Pink Shrimp Biomass Consumed

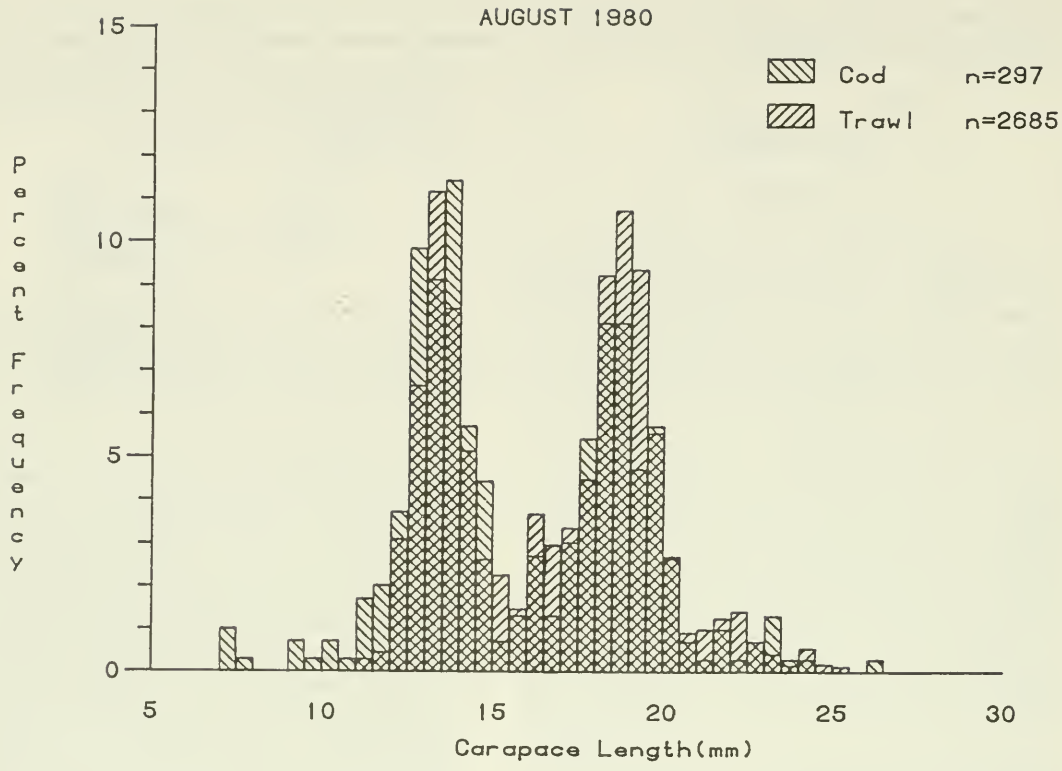
The estimated pink shrimp biomass in Pavlof Bay decreased by 1,501 t between the May and September surveys in 1981. During this period we estimated that Pacific cod consumed between 142 and 875 t of pink shrimp. Since Pavlof Bay is believed to contain a geographically isolated stock of pink shrimp (Anderson 1981) and because the bay was closed to shrimp fishing in 1981, cod predation is responsible for at least part of the biomass decline.

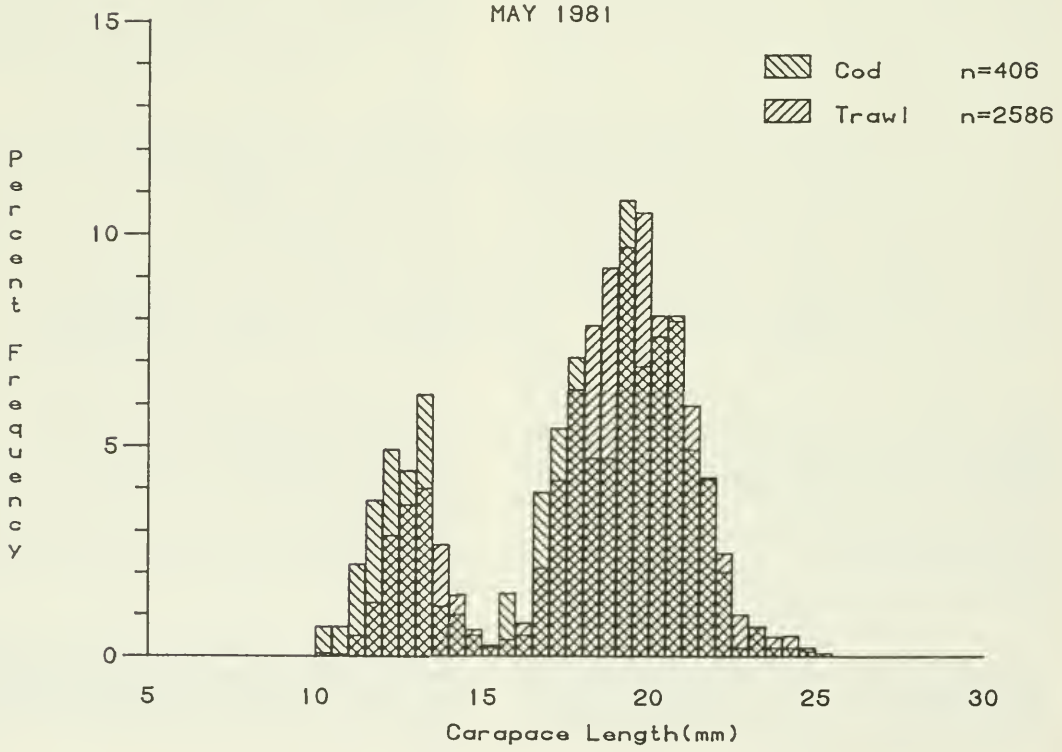
The estimate of pink shrimp biomass consumed over the 112-d period using the May survey data was 733 t more than was estimated using September data. Two of the parameters used to calculate consumption estimates were responsible for this difference. In May the mean weight of pink shrimp consumed daily by one cod was about double the amount in September. Pink shrimp were more abundant and made up a larger percentage of the diet in May than in September. Additionally, cod biomass was estimated to be almost three times higher in May than it was in September causing the consumption estimate to be higher in May (Table 5).

We belive that consumption of pink shrimp by cod probably lies toward the high end of the calculated range (142-875 t). Biomass estimates were probably conservative for pink shrimp and Pacific cod. Biomass was calculated on the assumption that all cod and shrimp were on bottom and all those in the path of the trawl were caught. This is not true for cod or shrimp. For example, Edwards (1968) reported that up to 49% of the gadoids in the path of a trawl avoid capture. Also, an estimate of the catchability of shrimp with the high-opening shrimp trawl was about 56% (Alaska Department of Fish and Game 1982[4]). If the cod biomass estimate was conservative, the consumption of pink shrimp by cod would be higher than calculated. Further, if the pink shrimp biomass estimate was conservative, the calculated

[3]Gaffney, F. G. 1977. Kodiak pandalid shrimp research. Commercial Fisheries Research and Development Act, Project No. 5-36-R. Unpubl. manuscr., 76 p. National Marine Fisheries Service, NOAA, Wash., DC 20235.

[4]Westward Region Shellfish Staff, Alaska Department of Fish and Game. 1982. Westward Region Shrimp Fishery Management Plan. Unpubl. manuscr., 70 p. Alaska Department of Fish and Game, Kasheruaroff, Mission Road, P.O. Box 686, Kodiak, AK 99615.


AUGUST 1980
Cod n=297
Trawl n=2685
Percent Frequency
15
10
5
0
5
10
15
20
25
30
Carapace Length(mm)


MAY 1981
Cod n=406
Trawl n=2586
Percent Frequency
15
10
5
0
5
10
15
20
25
30
Carapace Length(mm)

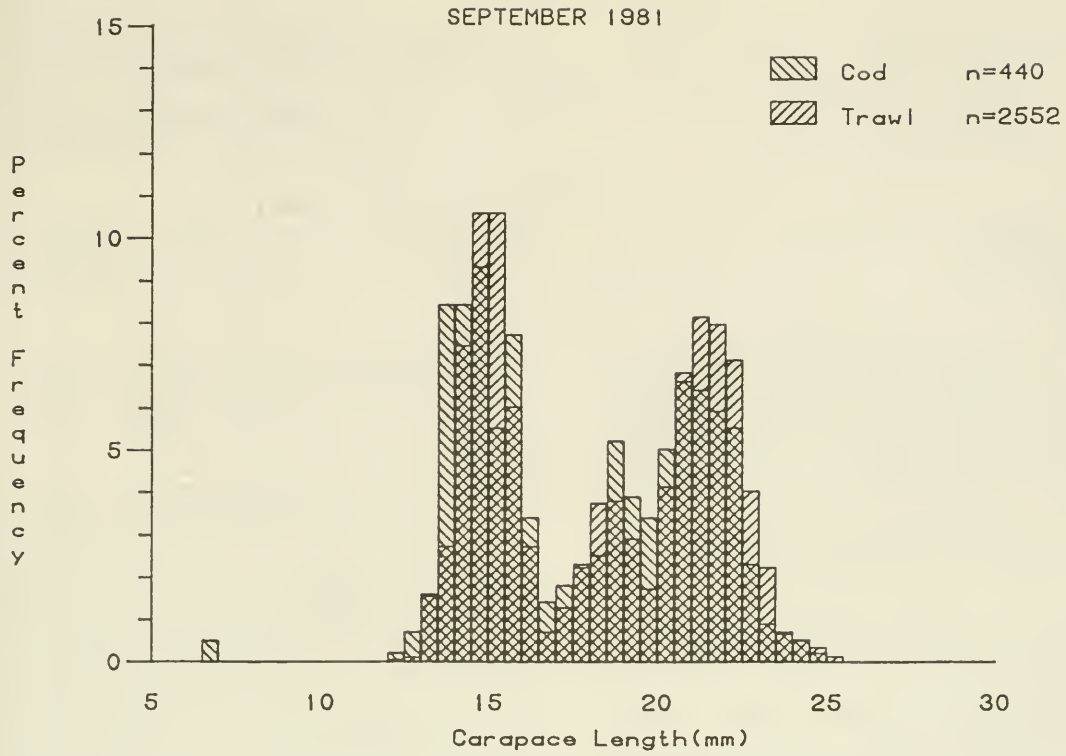


FIGURE 3.—Size distribution of pink shrimp from trawl samples and Pacific cod stomachs for August 1980 and May and September 1981.

biomass decline of pink shrimp between May and September 1981 would also be greater.

Pacific cod are probably feeding on pink shrimp in Pavlof Bay the entire year although the largest concentrations of cod are likely to occur from spring through fall. Trawl survey data from Pavlof Bay indicate that cod biomass decreased from 93 t in September 1978 to 20 t in February 1979 and then increased to 371 t in May 1979. Pacific cod are migratory; they move to shallow areas (<90 m) in spring to feed and return to deeper areas (165-247 m) offshore in fall or winter to spawn (Moiseev 1953). The majority of Pavlof Bay is <90 m deep which is not preferred winter habitat.

Although we believe that Pacific cod predation has an effect on the present reduced population of pink shrimp, predation probably was not the primary reason for the initial decline of pink shrimp in Pavlof Bay that began in 1977. At that time Pacific cod abundance was just beginning to increase (Fig. 2). Fishing removed about 3,819 t (calculated from ADF&G commercial catch data and NMFS survey data) of pink shrimp between the 1977 and 1978 surveys, which was 30% of the estimated available biomass in 1977. This harvest and the dying out of the strong 1971 year class (Anderson 1981) were probably responsible for most of that initial decrease. Cod predation did become a factor, however, once the pink shrimp resource was reduced. This impact on pink shrimp appears substantial despite the reduction of cod in Pavlof Bay (Fig. 2).

ADF&G (footnote 4) has reported diminishing pink shrimp stocks in other areas of the western Gulf of Alaska. Some areas that once contained high concentrations of pink shrimp experienced reductions in abundance at the same time as Pavlof Bay. In most areas, no increase in pink shrimp abundance was observed through 1982, though many areas were closed to fishing. Like Pavlof Bay, these other areas experienced an increase in Pacific cod abundance about the same time as pink shrimp populations were declining. Cod predation may play a role in keeping these reduced pink shrimp stocks from rebuilding to former levels.

ACKNOWLEDGMENTS

Thanks to Pete Jackson and Dave Jackson, Alaska

Department of Fish and Game, for collecting the May 1981 stomach samples.

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VERTICAL DISTRIBUTION OF ICHTHYOPLANKTON OFF THE OREGON COAST IN SPRING AND SUMMER MONTHS

GEORGE W. BOEHLERT,[1] DENA M. GADOMSKI,[2] AND BRUCE C. MUNDY[1]

ABSTRACT

Day and night discrete-depth tows were taken off the Oregon coast in spring and summer months to assess the vertical distribution of ichthyoplankton in nearshore waters. Over 1,000 larvae representing 33 taxa of both coastal and offshore ichthyoplankton assemblages were taken; *Psettichthys melanostictus* was the most abundant coastal species and *Lyopsetta exilis* the most abundant offshore species. Larvae were generally most abundant at 10-30 m, near the seasonal thermocline in both day and night collections. Larval abundance in July was much higher than in April-May collections. Limited evidence for diel vertical migration suggests that *Psettichthys melanostictus* moves to surface waters at night and *Gadus macrocephalus* moves to deeper water at night. No trends of changes in depth distribution were observed with increasing size.

Knowledge of the vertical distributions of larval fishes is crucial to full understanding of their biology and to understanding the results of ichthyoplankton surveys (Ahlstrom 1959; Kendall and Naplin 1981). The interaction between vertical distributions and physical processes can have important effects on onshore-offshore distributions of planktonic organisms in upwelling regions such as the coastal northeastern Pacific (Peterson et al. 1979; Parrish et al. 1981; Wroblewski 1982; Rothlisberg et al. 1983). Near-surface distribution, for example, may result in shoreward transport in slicks associated with internal waves (Shanks 1983). In the coastal region off Oregon, the only information on larval fish vertical distribution is a comparison between abundances of *Parophrys vetulus* and *Isopsetta isolepis* larvae from neuston and oblique bongo net tows (Laroche and Richardson 1979) and one 24-h study with stratified samples taken by bongo nets without opening-closing devices (Richardson and Pearcy 1977). With the exceptions of the classic study by Ahlstrom (1959) and recent studies by Brewer et al. (1981) and Schlotterbeck and Connally (1982), little else is known about the vertical distribution of larval fishes in northeastern Pacific coastal waters. In this paper, we present information on vertical distributions of larval fishes off Oregon.

METHODS

Six series of samples were collected in 1982, four during daylight (30 April, 14 May, 2 and 13 July) and two during night (2 and 6-7 July). The first two series (30 April, 14 May) were taken at station NH10, 10 nmi (18.5 km) off Newport, OR, on the Newport hydroline (lat. 44°40'N; Fig. 1). All others were collected at NH5 (9.2 km offshore). Each sample series consisted of a variable number of tows at discrete depth strata from the surface to within about 4 m of the bottom (Table 1).

Tows were stepped oblique in five intervals of 3 min each, resulting in a total sampling time of 15 min in each 5 or 10 m depth stratum. The sampler was an opening-closing Tucker trawl (Clarke 1969) with three nets and a double-release mechanism operated by messengers. The nets were 0.505 mm mesh (Nitex[3]) with a 1 m^2 mouth; all tows were at a wire angle of 45° at approximate tow speeds from 0.9 to 1.1 m/s. At this angle, effective mouth area of the net is 0.71 m^2. An uncontaminated, discrete depth sample was collected in the second net by lowering the trawl with the first net open, opening the second net for the desired sampling time, and retrieving the trawl with the third net open. Water volumes filtered were estimated with General Oceanics flowmeters mounted in the center of each net. Volumes of water filtered usually ranged between 250 and 450 m^3/sample. Temperature and salinity data were collected throughout the water column on each cruise using Niskin bottles to collect

[1]College of Oceanography and Marine Science Center, Oregon State University, Newport, OR; present address: Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[2]College of Oceanography and Marine Science Center, Oregon State University, Newport, OR; present address: Section of Fishes, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, CA 90007.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

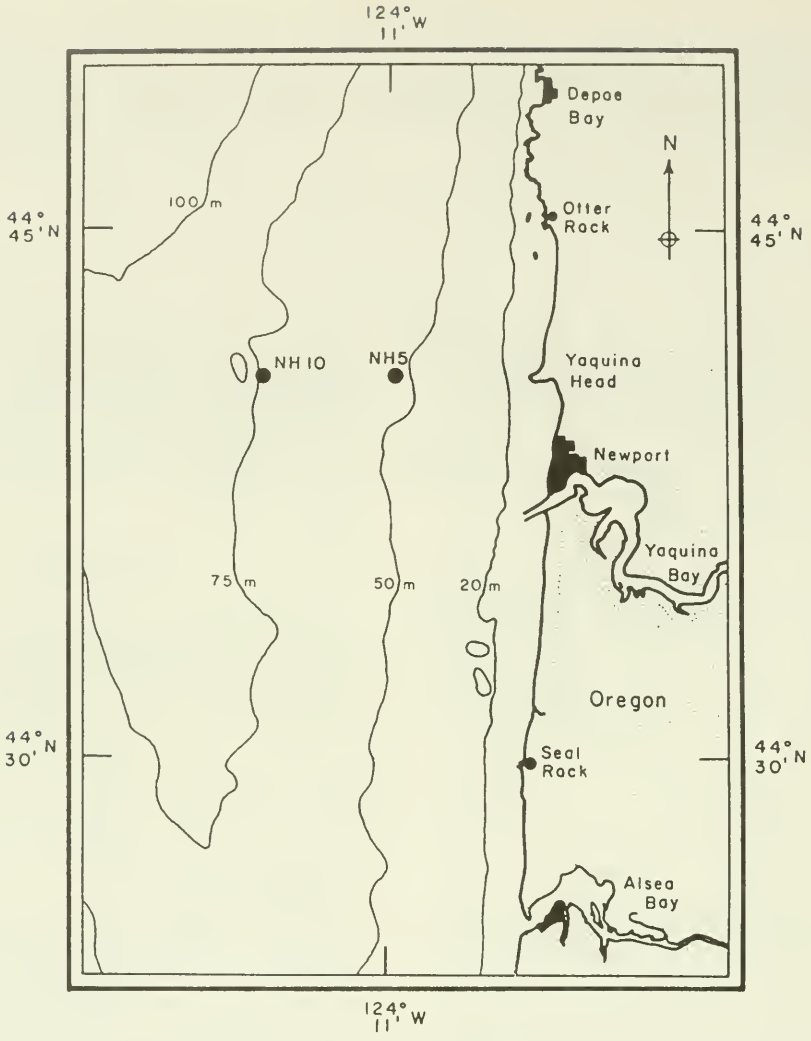

FIGURE 1.—Locations of the sampling conducted during the present study. NH5 and NH10 indicate the stations used.

TABLE 1.—Number of tows per depth stratum with total volumes filtered. (Asterisk indicates that for subsequent analysis the NH10 day sample in the two deepest categories were combined with the 50-60 m stratum.) Sample times were as follows: Day—4/30, 1018-1547; 5/14, 0808-1600; 7/2, 0608-0907; 7/13, 0554-1048; night—7/2, 0016-0514, 7/6-7/7, 2330-0410.

	Day						Night		
	NH10			NH5			NH5		
Depth (m)	4/30	5/14	Total volume filtered (m^3)	7/2	7/13	Total volume filtered (m^3)	7/2	7/6-7/7	Total volume filtered (m^3)
0-5	2	2	1,682.7	2	2	1,392.6	2	2	1,574.8
5-10	2	2	1,783.7	2	2	1,451.2	2	2	1,575.7
10-20	2	2	1,595.7	1	2	862.9	2	2	1,292.9
20-30	2	2	1,796.7	1	2	929.3	2	2	1,237.6
30-40	1	2	1,415.8	1	2	920.5	1	2	1,184.0
40-50	1	2	1,488.1	1	2	920.9	1	2	1,034.8
50-60	1	2	1,891.2	1	2	671.3	1	1	808.3
60-70*	1	1	930.0	—	—	—	—	—	—
70-80*	—	1	704.8	—	—	—	—	—	—

water samples at 5 to 10 m intervals or using a self-contained Applied Microsystems CTD-12. The salinities of water bottle samples were determined in the laboratory using a Guideline 8400 autosalinometer. The CTD salinities from 13 July were not used because of suspected machine malfunction. The CTD temperatures from 13 July agreed with surface bucket temperatures and were used in our study.

Plankton samples were preserved at sea in 10% buffered Formalin. Samples were sorted for fish larvae in the laboratory using a dissecting microscope. Larvae were identified to the lowest possible taxon, measured (standard length), and stored in 5% buffered Formalin.

Larval abundances were calculated as number per 1,000 m^3 for each tow. The six sampling series were combined into three data sets, spring daytime samples (30 April and 14 May, NH10), summer daytime (2 and 13 July, NH5), and summer nighttime (2 and 6-7 July, NH5). In April and May the salinity profiles closely paralleled each other, with lower salinity at the surface, 30.5-31.0‰, than in deeper water, where salinities gradually increased to about 33-34‰ (Fig. 2a). Water temperatures above 50 m

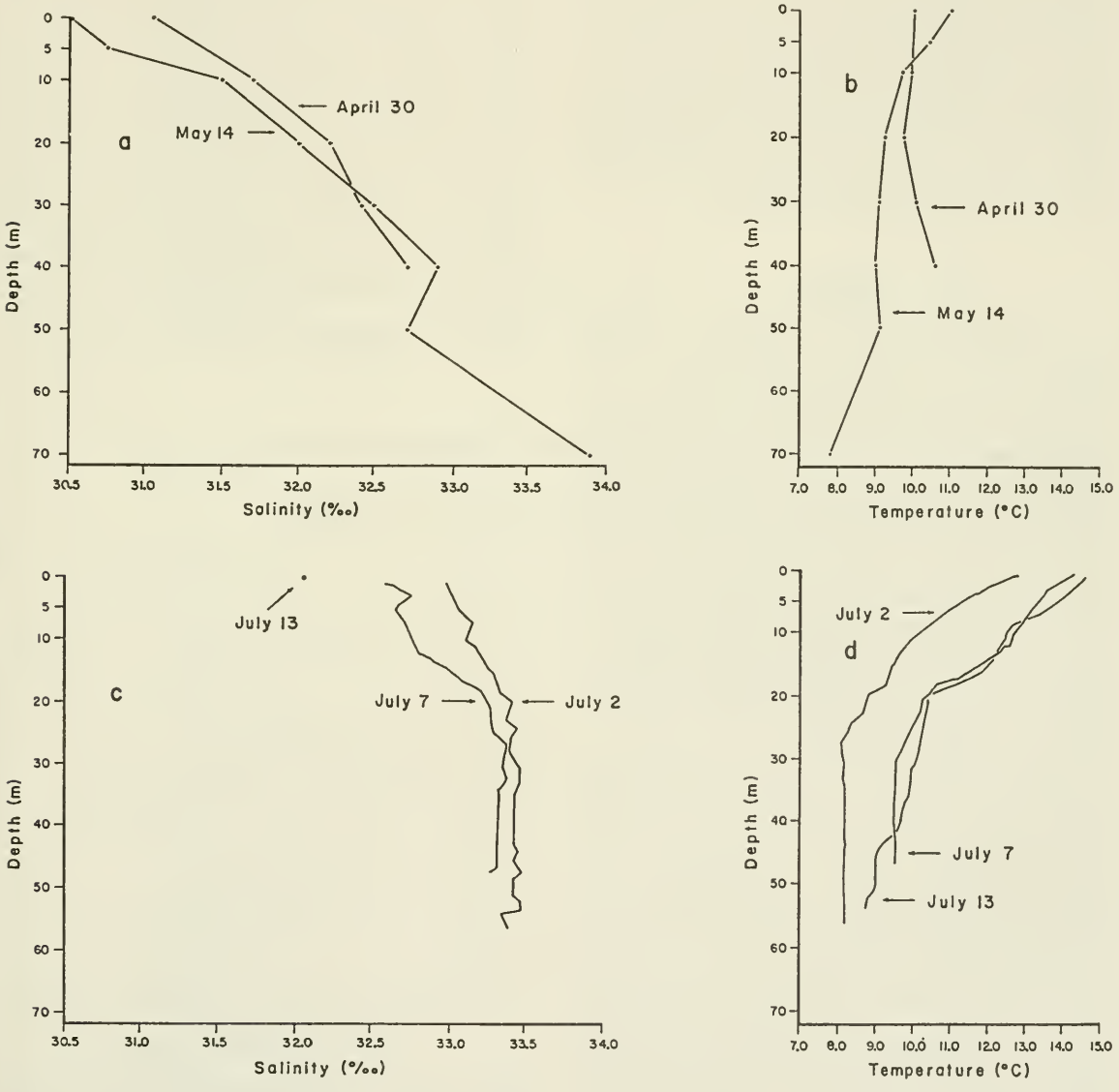

FIGURE 2.—Salinity and temperature profiles during the collections. a. Salinity profiles during the spring collections. b. Spring temperature profiles. c. Summer salinity profiles. d. Summer temperature profiles.

in April and May were about 9°-11°C (Fig. 2b). No thermocline was present. Thus, hydrographic regimes support grouping April and May samples together. Temperature and salinity profiles in April and May were typical for the winter Oregon hydrographic regime prior to the onset of late spring-early summer upwelling (Huyer 1977).

In July the salinity and temperature profiles differed from those in April and May (Figs. 2c, d). Salinities were more uniform in summer than spring throughout the water column, ranging from 32.0‰ at the surface to 33.4‰ below about 20 m (Fig. 2c). The temperature gradient in July was greater than in April and May due to warmer surface waters (Fig. 2d). Surface temperatures ranged from 12.8° to 14.6°C, decreasing with depth to about 8.2°-9.6°C at 40 m. A thermocline was present at about 10-20 m. Temperature and salinity profiles in July were typical of the summer Oregon hydrographic regime (Huyer 1977). Surface temperatures suggest that samples were not taken during active upwelling.

RESULTS

In this study, a total volume of 29,145.5 m^3 was filtered and 1,007 larvae, representing 33 taxa, were enumerated from 75 discrete depth tows. Larvae were most abundant in summer, with an abundance peak 10-30 m deep during daytime and 20-30 m deep during nighttime (Fig. 3). In spring, larvae were distributed relatively uniformly throughout the water column below 5 m with small abundance peaks at 10-20 and 40-50 m. During daytime in both spring and summer, larvae were least abundant at the surface (0-5 m), although abundance at the surface increased at night. The depth distribution at night also differed in having a secondary abundance peak near the bottom (50-60 m) and greater overall larval abundance than during the day.

The larval fish species were categorized as coastal (most abundance 2-28 km from the coast, see Tables 2, 3, and 4), or offshore (most abundant 37-111 km from the coast, see Tables 5, 6, and 7), according to larval assemblages described by Richardson and Pearcy (1977). Most larvae in this study were of the coastal assemblage because samples were collected at NH5 and NH10 (9.2 and 18.5 km from the coast, respectively). The spawning seasons of the dominant species off Oregon are discussed in Mundy (1984); most of the fall-winter spawning species were not represented in this study. Since many species were not abundant enough to demonstrate trends, only the dominant species will be discussed below.

Coastal Assemblage

Gadus macrocephalus, *Microgadus proximus*, *Isopsetta isolepis*, and *Psettichthys melanostictus* larvae were abundant in all three sampling periods (Tables 2, 3, 4, Fig. 4). *Gadus macrocephalus* larvae were most abundant during the day at 20-30 m in both spring and summer, but were very abundant in the deepest stratum (below 50 m) in night samples (Fig. 4). *Microgadus proximus* larvae do not show as clear a trend, but were most abundant in deeper water during summer, particularly at nighttime. In spring they were distributed throughout the water column. *Isopsetta isolepis* and *P. melanostictus* were also most abundant in nighttime samples. More *I. isolepis* larvae were found at 10-20 m in spring, whereas in summer they were collected throughout the water column, with abundance peaks near the bottom. *Psettichthys melanostictus* larvae were more abundant in summer than spring samples. During daytime in summer, *P. melanostictus* were most abundant below 10 m, whereas at nighttime, although found throughtout the water column, they were most abundant in waters shallower than 10 m (Fig. 4).

Seasonal abundance changes were observed for

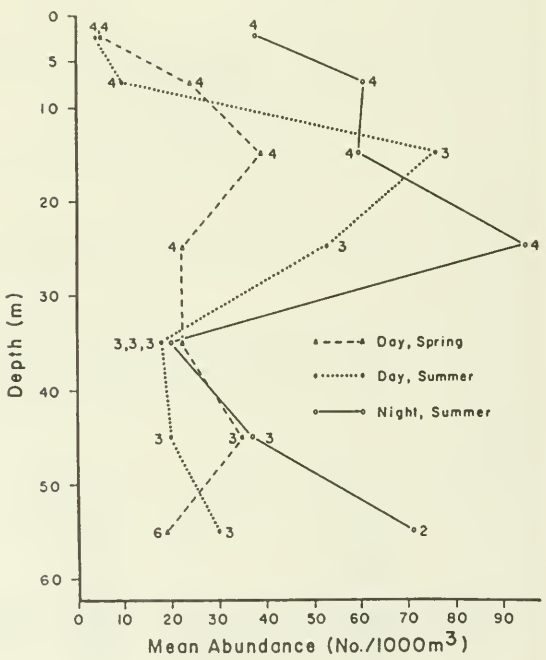

FIGURE 3.—Overall larval abundance (larvae per 1,000 m^3) for all collections. Numbers adjacent to data points indicate the number of samples taken.

TABLE 2.—Mean abundances (number per 1,000 m^3) for coastal larval species from spring (day only) samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Clupeidae								
Clupea harengus	—	—	1.76	2.36	1.25	0.75	—	0.87
Osmeridae								
Undetermined spp.	—	1.85	5.02	1.22	1.51	1.16	0.23	1.57
Gadidae								
Gadus macrocephalus	1.14	0.53	5.69	7.59	2.91	—	0.89	2.68
Microgadus proximus	1.13	2.04	3.87	2.97	0.73	2.95	0.45	2.02
Cottidae								
Artedius fenestralis	—	—	—	—	—	—	—	—
Artedius harringtoni	—	—	—	—	—	0.75	0.41	0.17
Artedius meanyi	—	—	—	—	—	—	0.44	0.06
Clinocottus embryum	—	—	—	—	—	—	—	—
Cottus asper	—	0.53	—	—	—	—	—	0.08
Radulinus asprellus	—	—	—	—	—	—	2.60	0.37
Agonidae								
Odontopyxis trispinosa	—	—	—	—	—	—	0.23	0.03
Cyclopteridae spp. 1	—	—	—	0.74	2.29	3.64	0.45	1.02
Undetermined spp.	—	—	—	0.47	—	—	—	0.07
Bathymasteridae								
Ronquilus jordani	—	0.59	—	—	—	—	—	0.08
Ptilichthyidae								
Ptilichthys goodei	—	—	0.94	—	—	—	—	0.13
Bothidae								
Citharichthys stigmaeus	—	—	—	—	0.73	—	0.87	0.23
Pleuronectidae								
Isopsetta isolepis	0.49	1.79	7.78	2.86	—	1.29	0.66	2.12
Lepidopsetta bilineata	—	0.59	0.94	—	—	—	—	0.22
Parophrys vetulus	—	0.59	1.76	—	—	—	0.45	0.40
Psettichthys melanostictus	1.48	5.46	5.58	—	0.73	—	0.44	1.96

TABLE 3.—Mean abundances (number per 1,000 m^3) for coastal larval species from summer day samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Clupeidae								
Clupea harengus	—	—	—	—	—	—	—	—
Osmeridae								
Undetermined spp.	—	—	—	—	—	—	3.69	0.53
Gadidae								
Gadus macrocephalus	—	—	1.38	12.01	1.08	1.09	—	2.22
Microgadus proximus	—	—	2.01	1.01	—	3.28	3.49	1.40
Cottidae								
Artedius fenestralis	—	—	1.00	1.15	—	—	—	0.31
Artedius harringtoni	—	0.68	4.54	3.30	2.18	2.19	3.39	2.33
Artedius meanyi	—	—	3.38	2.02	1.10	—	—	0.93
Clinocottus embryum	—	—	—	—	—	—	—	—
Cottus asper	—	0.53	—	—	—	—	—	0.08
Radulinus asprellus	—	—	—	—	—	—	—	—
Agonidae								
Odontopyxis trispinosa	—	—	—	1.01	—	—	—	0.14
Cyclopteridae spp. 1	—	—	—	2.22	2.16	—	—	0.63
Undetermined spp.	—	—	2.16	4.18	1.08	2.18	6.05	2.24
Bathymasteridae								
Ronquilus jordani	0.63	0.70	2.01	1.01	—	—	—	0.62
Ptilichthyidae								
Ptilichthys goodei	—	—	—	—	—	—	—	—
Bothidae								
Citharichthys stigmaeus	—	—	1.00	—	—	—	—	0.14
Pleuronectidae								
Isopsetta isolepis	—	—	2.07	1.01	2.20	—	4.82	1.44
Lepidopsetta bilineata	—	—	—	—	—	—	—	—
Parophrys vetulus	—	—	—	—	—	—	—	—
Psettichthys melanostictus	0.98	2.03	22.98	7.48	3.24	3.26	11.18	7.31

TABLE 4.—Mean abundances (number per 1,000 m^3) for coastal larval species from summer night samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Clupeidae								
Clupea harengus	—	—	—	—	—	—	—	—
Osmeridae								
Undetermined spp.	—	4.42	15.15	4.56	—	0.75	1.12	3.71
Gadidae								
Gadus macrocephalus	—	—	—	0.82	3.16	8.11	22.98	5.01
Microgadus proximus	0.66	0.61	—	4.66	1.95	3.29	6.91	2.58
Cottidae								
Artedius fenestralis	3.20	—	0.78	1.57	—	0.75	2.60	1.27
Artedius harringtoni	1.35	4.41	5.44	11.30	0.73	1.27	1.40	3.70
Artedius meanyi	0.66	4.48	0.71	4.12	0.74	1.01	3.62	2.19
Clinocottus embryum	0.66	—	—	—	—	—	—	0.09
Cottus asper	—	—	—	—	—	—	—	—
Radulinus asprellus	—	—	—	—	—	—	—	—
Agonidae								
Odontopyxis trispinosa	—	—	—	—	—	—	2.50	0.36
Cyclopteridae spp. 1	—	—	0.77	0.79	—	—	—	0.22
Undetermined spp.	—	—	—	3.96	0.73	—	4.74	1.35
Bathymasteridae								
Ronquilus jordani	—	—	0.71	1.70	—	1.27	—	0.53
Ptilichthyidae								
Ptilichthys goodei	—	—	—	—	—	—	—	—
Bothidae								
Citharichthys stigmaeus	—	—	—	0.74	0.74	—	—	0.21
Pleuronectidae								
Isopsetta isolepis	—	2.57	1.63	6.50	2.64	10.90	1.12	3.62
Lepidopsetta bilineata	—	—	—	—	—	—	—	—
Parophrys vetulus	0.66	—	0.71	—	—	—	—	0.20
Psettichthys melanostictus	24.63	31.37	13.65	18.86	7.78	6.07	6.91	15.61

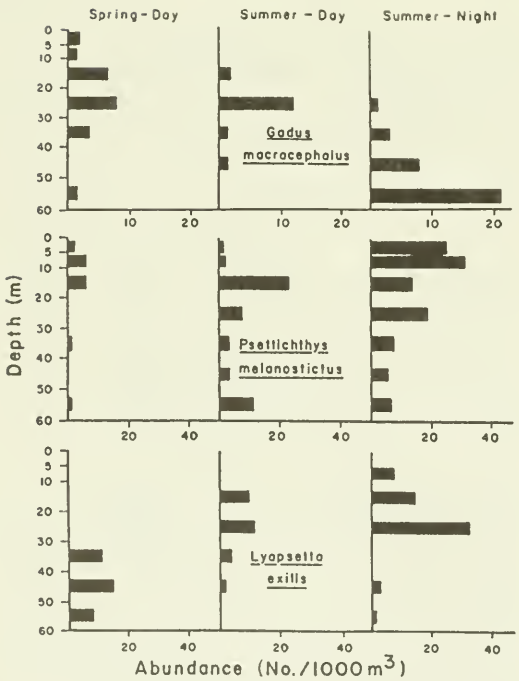

FIGURE 4.—Vertical abundance patterns of the three most abundant taxa (*Gadus macrocephalus*, *Psettichthys melanostictus*, and *Lyopsetta exilis*) during the three sampling periods.

Artedius and cyclopterid species. *Artedius fenestralis*, *A. harringtoni*, and *A. meanyi* were taken almost exclusively in the summer sampling period. All species were most abundant in nighttime samples. During the day, *A. harringtoni* larvae were distributed relatively uniformly throughout the water column from about 10 to 60 m, whereas at night most larvae were taken from the 5-30 m depth strata. Most cyclopterid larvae collected in spring were the larval type referred to as Cyclopteridae spp. 1 by Richardson and Pearcy (1977). Other cyclopterid species were more abundant in summer. Most cyclopterid larvae were collected below 20 m during both night and day, and in summer were abundant at the deepest sampling depths.

Osmerid larvae of undetermined species had a unique distribution pattern. They were abundant during spring, rare during summer daytime samples, and most abundant during summer nighttime samples. During both spring and summer, larvae were most abundant at the 10-20 m depth stratum.

Offshore Assemblage

Spring to summer differences in abundance patterns were more distinct for offshore larval species as compared with coastal species (Tables 5, 6, 7).

TABLE 5.—Mean abundances (number per 1,000 m^3) for offshore larval species from spring (day only) samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Offshore								
Engraulidae								
Engraulis mordax	—	—	—	—	—	—	—	—
Bathylagidae								
Bathylagus ochotensis	—	—	0.56	—	0.78	7.28	0.87	1.36
Bathylagus pacificus	—	—	—	—	—	—	0.22	0.03
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	0.75	—	0.11
Protomyctophum thompsoni	—	—	—	—	—	1.74	1.19	0.42
Stenobrachius leucopsarus	0.49	6.79	2.76	0.47	—	—	—	1.50
Bythitidae								
Brosmophycis marginata	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes spp.	—	2.73	1.06	1.49	—	—	—	0.75
Bothidae								
Citharichthys sordidus	—	—	—	—	—	—	—	—
Pleuronectidae								
Glyptocephalus zachirus	—	—	1.06	—	—	—	—	0.15
Lyopsetta exilis	—	—	—	—	11.27	14.9	8.56	4.96
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	—	1.49	—	—	—	0.21

TABLE 6.—Mean abundances (number per 1,000 m^3) for offshore larval species from summer day samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Offshore								
Engraulidae								
Engraulis mordax	0.98	2.13	—	—	—	—	—	0.44
Bathylagidae								
Bathylagus ochotensis	—	—	—	—	—	—	—	—
Bathylagus pacificus	—	—	—	—	—	—	—	—
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	—	—	—
Protomyctophum thompsoni	—	—	—	—	—	—	—	—
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—
Bythitidae								
Brosmophycis marginata	1.49	0.73	—	—	—	—	—	0.32
Scorpaenidae								
Sebastes spp.	—	0.65	3.03	1.08	1.10	—	—	0.84
Bothidae								
Citharichthys sordidus	—	0.73	—	—	—	—	—	0.10
Pleuronectidae								
Glyptocephalus zachirus	—	2.11	19.55	4.52	—	—	—	3.74
Lyopsetta exilis	—	—	10.03	11.53	4.38	2.13	—	4.01
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	—	—	—	1.10	—	0.16

Only *Sebastes* and *Lyopsetta exilis* larvae were abundant in all three sampling periods. *Sebastes* larvae were most abundant in nighttime samples, when they were mainly collected in shallow water (0-20 m). In both spring and summer daytime samples they were also in relatively shallow waters (5-40 m), although they were not abundant at the shallowest stratum (0-5 m). During day, *L. exilis* larvae were distributed in deeper water, particularly in spring, when all larvae were collected below 30 m (Fig. 3). At night, most *L. exilis* were shallower, between 5 and 30 m.

Two species, *Bathylagus ochotensis* and *Stenobrachius leucopsarus*, were collected only in spring samples. These two species were predominantly collected at different depths with *B. ochotensis* found

TABLE 7.—Mean abundances (number per 1,000 m^3) for offshore larval species from summer night samples.

Species	Depth (m) 0-5	5-10	10-20	20-30	30-40	40-50	>50	Mean
Offshore								
Engraulidae								
Engraulis mordax	4.09	3.76	—	—	—	—	—	1.12
Bathylagidae								
Bathylagus ochotensis	—	—	—	—	—	—	—	—
Bathylagus pacificus	—	—	—	—	—	—	—	—
Myctophidae								
Protomyctophum crockeri	—	—	—	—	—	—	—	—
Protomyctophum thompsoni	—	—	—	—	—	—	—	—
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—
Bythitidae								
Brosmophycis marginata	—	—	—	—	—	—	—	—
Scorpaenidae								
Sebastes spp.	3.86	0.68	2.38	0.82	—	—	1.12	1.27
Bothidae								
Citharichthys sordidus	—	—	0.78	—	0.74	1.27	10.27	1.87
Pleuronectidae								
Glyptocephalus zachirus	0.66	0.68	0.77	0.91	—	—	—	0.43
Lyopsetta exilis	—	8.28	15.05	32.99	—	3.53	1.12	8.71
Coastal-Offshore								
Pleuronectidae								
Hippoglossoides elassodon	—	—	0.71	—	—	—	1.12	0.26

in deeper water (40-50 m) and *S. leucopsarus* in shallow water (5-20 m).

Two species of larval flatfishes and *Engraulis mordax* were collected only in summer samples. *Glyptocephalus zachirus* were most abundant during day at 5-30 m, and *Citharichthys sordidus* at night below 50 m. *Engraulis mordax* larvae were collected only above 10 m. *Engraulis mordax* were most abundant at night when more than half were in very shallow waters, <5 m. During the day, more *E. mordax* were found at 5-10 m than at 0-5 m.

A relationship between larval size and depth was not evident for any species. Because of the low abundances of larvae, however, this relationship could not be adequately considered for most species. A change in larval size with season was demonstrated for the most abundant species (Table 8), with mean larval standard lengths of all species greater in summer than in spring samples. There were no obvious differences between the size of larvae caught in day and night summer samples.

DISCUSSION

Peak abundances of all taxa combined occurred at 10-30 m on all sample dates (Fig. 3) and characterized several individual taxa during the day, including *Clupea harengus*, Osmeridae, *Gadus macrocephalus*, *Sebastes* spp., and *Parophrys vetulus*, as well as *Lyopsetta exilis* and *Psettichthys melanostictus* in the summer. The 10-30 m depth range bracketed the lower boundary of the seasonal thermocline in July, although no thermocline was present in April-May (Fig. 2). This trend for the peak abundance of fish larvae to be centered near the thermocline is similar to that found in other regions (Ahlstrom 1959; Miller et al. 1963; Kendall and Naplin 1981).

The trend for most larvae to be found in midwater was similar to that described by Brewer et al. (1981) for their deepest stations off southern California. We did not find large concentrations of larvae near the bottom as they did, except at night, when gadids, cottids, cyclopterids, and pleuronectids were abundant. Our sampling gear was ineffective just above the bottom as compared with the roller-equipped gear used by Brewer et al. (1981).

Richardson and Pearcy (1977) found larvae to be most abundant at 0-10 m and least abundant at 51-100 m during late May off Oregon. We found larvae to be most abundant at 10-30 m. This difference may be due to differences in hydrography and station locations. Their station was 18 km offshore, closer to the shelf break where the depth of water was over 150 m deep. The faunal composition in each study was also different. Richardson and Pearcy (1977) captured more specimens of several surface-associated taxa than we did, including large *Clupea harengus*, *Stenobrachius leucopsarus*, *Ronquilus jordani*, and *Ammodytes hexapterus*. We captured higher densities of deeper dwelling taxa, including gadids and cottids. Several taxa taken in both studies had different distributions in each, including *Sebastes*

TABLE 8.—Ranges and mean standard lengths (mm) for dominant fish larvae. *N* = number of larvae; Min. = minimum; Max. = maximum.

Species	Spring: Day				Summer: Day				Summer: Night			
	N	Min.	Mean	Max.	*N*	Min.	Mean	Max.	*N*	Min.	Mean	Max.
Coastal												
Clupea harengus	10	7	8.2	9	0	—	—	—	0	—	—	—
Osmerid	17	3	7.1	17	3	29	33.1	38	35	23	31.8	40
Gadus macrocephalus	29	8	10.8	20	17	9	13.6	17	28	9	13.3	19
Microgadus proximus	22	6	10.9	19	9	11	21.3	36	18	6	18.4	33
Artedius fenestralis	0	—	—	—	2	11	12.0	13	8	10	11.6	13
Artedius harringtoni	2	6	6.5	7	15	5	8.2	13	33	5	8.6	14
Artedius meanyi	1	—	4.9	—	6	7	9.9	16	19	7	9.4	18
Radulinus asprellus	10	6	7.6	9	0	—	—	—	0	—	—	—
Liparid type 1	12	4	5.7	6	4	3	3.1	3	2	3	3.5	4
Liparid unknown	1	—	10.2	—	14	5	16.7	25	10	15	20.4	23
Ronquilus jordani	1	—	6.6	—	5	22	27.1	33	5	24	24.1	25
Isopsetta isolepis	22	4	8.9	21	9	10	20.0	23	28	7	16.1	23
Psettichthys melanostictus	—	3	7.0	22	41	9	20.0	27	150	8	20.8	28
Offshore												
Engraulis mordax	0	—	—	—	4	12	13.5	15	12	7	13.1	16
Bathylagus ochotensis	16	5	8.1	19	0	—	—	—	0	—	—	—
Stenobrachius leucopsarus	19	3	5.2	9	0	—	—	—	0	—	—	—
Sebastes spp.	8	4	4.7	6	6	4	14.6	18	12	12	16.0	18
Citharichthys sordidus	0	—	—	—	1	—	20.5	—	11	17	37.8	40
Glyptocephalus zachirus	2	13	25	37	22	14	29.9	39	4	22	34.5	50
Lyopsetta exilis	71	4	8.4	15	27	11	13.2	16	79	7	12.2	20

spp., Cyclopteridae spp. 1, and *Isopsetta isolepis*. These differences indicate the need for more extensive sampling before the variability of vertical distributions off Oregon can be understood, particularly as they relate to hydrographic conditions.

We found *Engraulis mordax* larvae entirely at 0-10 m. Brewer et al. (1981) found greater concentrations of *Engraulis* below 10 m, while Ahlstrom (1959) found *Engraulis* to be concentrated in the upper 23 m with some specimens occurring to 105 m. Off Oregon, *Engraulis* larvae are found concentrated at 0-20 m (Richardson 1973), in association with the Columbia River plume, a lens of warm, low salinity water usually 20-40 m deep (Richardson 1980). Our limited data suggest that *Engraulis mordax* larvae occur at depths that would place them within the plume, rather than beneath it or at its boundary. The vertical distribution suggests restriction to the warmest part of the water column (Fig. 2d); northern anchovies rarely spawn in waters with surface temperatures below 14°C (Lasker et al. 1981).

The seasonal differences in species composition between the April-May and July samples were those that would be expected in samples from winter and summer hydrographic regimes, except that *Artedius fenestralis* and *A. meanyi* have been taken in April and May of other years (Mundy 1984). The presence of *Clupea harengus*, *Radulinus asprellus*, myctophid, and bathylagid larvae only in April-May, during a winter hydrographic regime, is expected from previous studies (Richardson and Pearcy 1977; Mundy 1984).

Studies of day/night differences in the distribution of fish larvae are confounded by daytime avoidance of nets by larvae (Ahlstrom 1959). Daytime avoidance of nets is suggested in our study by the greater numbers of larvae taken during the night than day at all but two depth strata. The lack of length differences between larvae caught in day and night, however, and the fact that no taxa were taken only in night samples during July suggests that diurnal net avoidance was not related to taxon or size. The same comparisons with 70 cm bongo net samples (Richardson and Pearcy 1977) suggest that diurnal avoidance by large larvae was greater for bongo nets than for the Tucker trawl.

Evidence for vertical migration exists for several species in this study (Tables 3, 4, 6, 7). *Psettichthys melanostictus* abundance in surface waters (0-10 m) increased greatly at night (Fig. 4). *Engraulis mordax* were most abundant at 5-10 m than 0-5 m during the day, but more evenly distributed at night. This could be due either to vertical migration or net avoidance in the shallowest stratum during the day. Ahlstrom (1959), however, presented evidence for negative phototaxis by anchovy larvae, and Hunter and Sanchez (1976) demonstrated nighttime migration to the surface in larvae larger than 10 mm SL. Thus larvae migrate upwards at night, but are con-

strained to shallower water in the day as compared with the southern subpopulation.

The clearest case of vertical migration was that of *Gadus macrocephalus* (Tables 3, 4), which was most abundant at 20-30 m in the day and deeper than 50 m at night. The migration of this species was primarily responsible for the increased total abundance of larvae near the bottom at night (Fig. 3). This pattern of movement is similar to that observed for larval *Ammodytes personatus* by Yamashita et al. (1985), who suggested that this reverse vertical migration allowed feeding in daytime and avoidance of migrating predators at night. This nocturnal descent, not previously reported for *Gadus* larvae, should be confirmed with further sampling. *Gadus morhua* larvae 3.8-4.9 mm long move from deeper water in the day to 0-2 m at night, and descend in the water column with growth (Hardy 1978). Larvae of another gadid, *Melanogrammus aeglefinus*, are most common in the thermocline and their depth of greatest abundance fluctuates as the thermocline depth changes with rotary tidal currents, causing occasional descent in the water column at night (Miller et al. 1963).

Offshore taxa in Oregon coastal waters should occur in greatest numbers during onshore surface water transport during winter and early spring. This was true in our study for the mesopelagic Myctophidae and Bathylagidae, but not for other offshore assemblage taxa (Tables 5, 6, 7). Almost all of the bathylagid and myctophid larvae except *Stenobrachius leucopsarus* were found below 30 m. Ahlstrom's (1959) work confirms these general distributions; he found most larvae of the genera taken in this study (*Electrona* = *Protomyctophum*; *Lampanyctus* = *Stenobrachius*) at depths >56 m, beneath the thermocline, except *Stenobrachius*. He found *Stenobrachius* to have the shallowest distribution of all myctophid larvae in his study (0-41 m). Richardson and Pearcy (1977) also found *Stenobrachius* larvae to be in shallow waters (0-50 m) with many at 0-10 m during the day. The distribution of larval mesopelagic fishes, or other offshore taxa, cannot be related to the depth of onshore transport because virtually nothing is known about the depth of winter onshore transport off Oregon (Peterson et al. 1979; Huyer[4]). Both deep and surface dwelling larvae of mesopelagic fishes collected in our study appear to be transported onshore, however, suggesting that transport occurs over a broad depth range off Oregon.

[4]A. Huyer, Associate Professor, Oregon State University, Corvallis, OR 97331, pers. commun. 29 September 1983.

ACKNOWLEDGMENTS

This research was supported by NOAA Office of Sea Grant, Department of Commerce, under Grant No. NA81-D-00086. We thank M. Yoklavich, J. Shenker, and the crew of the RV *Sacajawea* for assistance in sampling. We also thank W. G. Pearcy and H. G. Moser for reviewing the manuscript.

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DOLPHIN HABITATS IN THE EASTERN TROPICAL PACIFIC

David W. K. Au and Wayne L. Perryman[1]

ABSTRACT

Research-ship surveys by the Southwest Fisheries Center provided information on the distributions of spotted, spinner, striped, and common dolphins in the eastern tropical Pacific. The main surveys were conducted from January to March during 1976, 1977, 1979, and 1980. Two ships were used per survey, and together they overlapped most areas in the eastern Pacific where dolphins and yellowfin tuna are jointly fished by purse seiners.

The spatial distribution of sightings and of sighting rate of these species show a complementarity to their patterns, although there is a broad overlap. Spotted and spinner dolphins occurred primarily in tropical waters north of the Equator, but also in the seasonal tropical waters south of the Galapagos Islands. These dolphins were relatively infrequent along the Equator, off Costa Rica, and northern South America. Common and striped dolphins tended to be more frequent in these same areas of less frequent spotted and spinner dolphins.

The differences in habitats of these two species pairs can be described in oceanographic terms. Spotted and spinner dolphins are primarily in Tropical Surface Water, centered off southern Mexico and extending westward along lat. 10°N, where thermocline "ridging" and relatively small annual variations in surface temperature are features. Common and striped dolphins appear to perfer equatorial and subtropical waters with relatively large seasonal changes in surface temperature and thermocline depth and with seasonal upwelling.

The species composition of various areas in the eastern tropical Pacific supports the contention of two major communities. South of where spotted and spinner dolphin schools predominate (along with Risso's, bottlenose, and rough-toothed dolphins), striped and common dolphins and also pilot whales become increasingly important. Observations along the Equator also suggest a fauna different from that of the Tropical Surface Water that is most characterized by spotted and spinner dolphins.

A trophic basis to these faunal differences is suggested by the interactions with fish and birds. Assuming the birds indicate co-occurring tuna, only the spotted and spinner dolphins are commonly found with fish. The distribution of these dolphins as they co-occur with bird flocks and tuna indicates that this interspecific association is confined primarily to the Tropical Surface Water and is a characteristic feature of its epipelagic community.

The eastern tropical Pacific Ocean supports productive tuna fisheries as well as an abundant and diverse cetacean fauna. Tuna fishermen there take advantage of the fact that tuna and dolphins frequently swim together. In the "porpoise-tuna" fishery for yellowfin tuna, *Thunnus albacares*, spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris*, are temporarily caught by purse seiners in order to take the associated tuna. Striped and common dolphins, *S. coeruleoalba* and *Delphinus delphis*, are caught to a lesser extent for the same reason. These dolphins suffer incidental mortality in the fishery and, because of the resulting concern, the Southwest Fisheries Center has been studying their populations to better advise on their management (Smith 1983). Learning about their habitats is one aspect of these studies.

Perrin (1975a), using the information collected mainly aboard tuna seiners, first showed that the geographic distributions of spotted, spinner, and striped dolphins in the eastern Pacific are extensive, stretching westward from the American coasts past long. 145°W at about lat. 10°N and also dipping south and southwest of the Galapagos Islands. Evans (1975) showed that the common dolphin occurs offshore of Central America to about long. 112°W and also along the Equator, westward past the Galapagos Islands. Recent summaries of available information (Au et al. 1979[2]; Scott 1981; Perrin et al. 1983) have shown that the distributions of these dolphins are even more extensive than originally perceived. Indeed the species have been reported from localities across the entire Pacific (Alverson 1981).

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[2]Au, D. W. K., W. L. Perryman, and W. F. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Admin. Rep. LJ-79-43, 59 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

The purpose of this paper is to describe the January-March distributions of schools of spotted, spinner, striped, and common dolphins as determined from research ship surveys. Being independent and distinct from data collected by observers aboard tuna seiners, these survey data enable a separate evaluation of habitats and ecological relationships. The distributions derived will be discussed in terms of habitat features and interspecific associations including those of other cetaceans, yellowfin tuna, and certain seabirds. We propose that two major cetacean communities can be recognized, centered broadly about the tropical and about the equatorial-subtropical surface water provinces (Fig. 1).

METHODS

The Southwest Fisheries Center conducted or participated in 17 research cruises studying cetaceans between 1976 and 1981. Eight major cruises were carried out between January and March of 1976, 1977, 1979, and 1980, with the NOAA ships *David Starr Jordan* and *Townsend Cromwell*. During these surveys, schools of all cetacean species encountered (at least 23 species in the areas of interest) were approached to allow close observation. The combined cruise tracks of these January-March surveys formed an extensive coverage of the eastern tropical Pacific and included areas not frequently searched by fishing vessels (Fig. 2). The latter are the equatorial waters and areas both south of lat. 8°N and west of long. 110°W. The cruise tracks during any particular year were chosen to investigate certain aspects of dolphin distribution, e.g., the intensive surveys during 1979 off southern Mexico and central America constituted a joint aircraft-ship survey of the nearshore habitat. The remaining other nine cruises were either for special studies or of ships of opportunity. In the latter case, the ships did not usually divert course to inspect cetacean schools that were sighted.

Cetacean observations from a research ship were conducted by scanning the waters ahead and to the sides of the ship through 20 × 120 mm USN MK-3

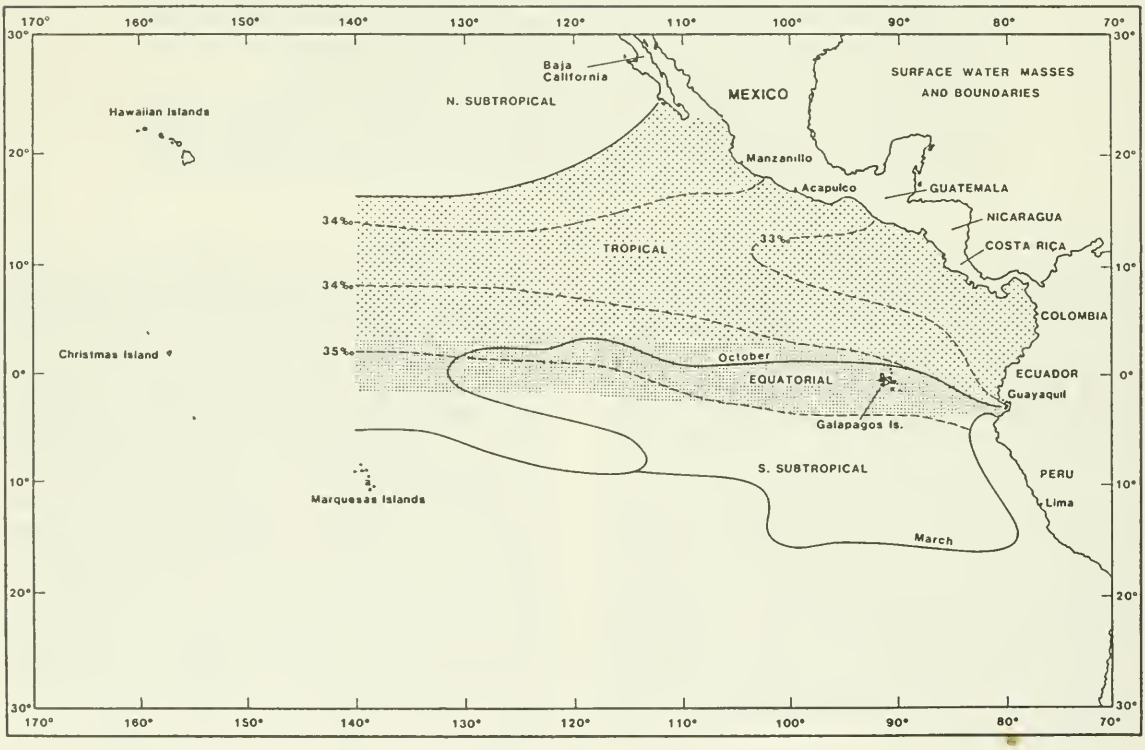

FIGURE 1.—Surface water masses and boundaries of the tropical ocean in the eastern Pacific, based on Wyrtki's (1964a, 1967) analysis to long. 140°W. Boundaries are a function of the 24°C surface isotherm and the 1°C/10 m thermocline gradient. Notice that in October the southern boundary to the eastern tropical ocean lies mostly north of the Equator, while in March this boundary lies far to the south so that southern subtropical waters become tropical.

or 25 × 150 mm Fuji binoculars, mounted both port and starboard either on or above the flying bridge. The sighting distance to the horizon was about 7.0 and 5.5 nmi for the *David Starr Jordan* and *Townsend Cromwell* respectively. Both ships cruised at about 10 kn (18.5 km/h). The cetacean search-day generally started at 0600 and ended 1800, with two teams, or watches, alternating. In 1976 and 1977 the watches were each 2 or 3 h long, depending on the ship. In 1979 and 1980 they were all standardized to 3 h. There were two experienced persons on each watch, who alternated each hour between the port and starboard binoculars. A third person sometimes helped in record keeping, obtaining supplementary data, and temporarily relieving the other watch members. The peripheral data collected included bathythermograms, surface temperature and salinity, weather observations, sighting condition measurements, sighting effort, and observations on fish and birds.

When a cetacean school was sighted, its angle relative to the ship's heading was measured and its distance from the ship estimated. The ship then approached the school for closer observation. School size was estimated and the species identified.

The reader is cautioned that the distributions to be described are based upon relatively few sightings of schools (Table 1) and that they pertain to the January-March season specifically. Though the pattern of sampling was widespread, the actual area surveyed was a very small fraction of the huge area

TABLE 1.—Summary of school sizes for spotted, spinner, striped, and common dolphins from the January-March research cruises of 1976, 1977, 1979, and 1980.

Species	Arithmetic			Geometric	
	n	$\bar{x}$	s	$\bar{x}$	s^1
Spotted[2]	157	148.52	300.93	65.55	3.56
Spotted and spinner	79	357.42	444.50	211.67	2.93
Spinner[3]	44	228.39	291.54	107.05	3.88
Striped	187	60.84	69.78	40.74	2.56
Common	98	261.16	484.64	108.47	3.72
Total[4]	565				

[1]Standard deviation factor for the geometric mean.
[2]Total spotted dolphin schools is 157 + 79 = 236.
[3]Total spinner dolphin schools is 44 + 79 = 123.
[4]Additionally, there were 838 school sightings of unidentified and other species of dolphins (Delphinidae) and 543 school sightings of whales (Balaenopteridae, Ziphiidae, and Physeteridae).

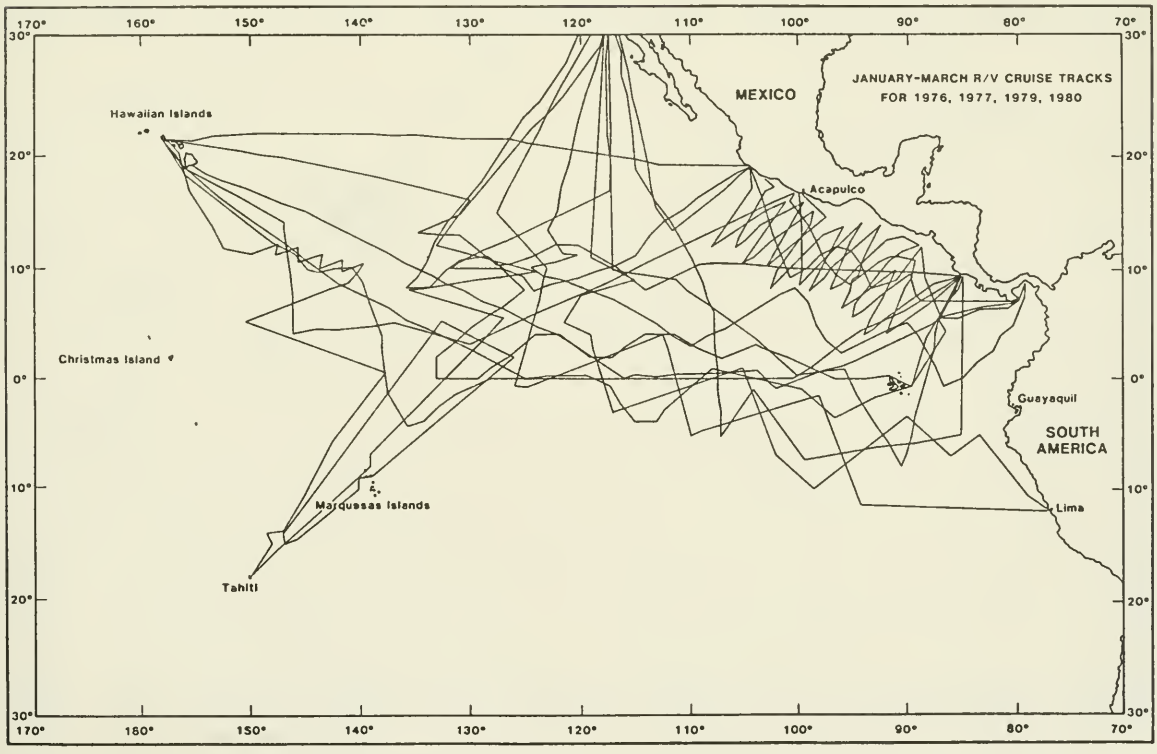

FIGURE 2.—Cruise tracks of the January-March cruises by RV *David Starr Jordan* and RV *Townsend Cromwell*. These cruises took place in 1976, 1977, 1979, and 1980.

of the eastern Pacific. The patterns of species distribution we describe will not always be obvious. Nevertheless there is evidence from other distribution studies, using data collected from the fishery, that these patterns are real (Perrin et al. 1983).

The results described in this paper are based upon our personal experiences at sea where the procedure of investigating all cetacean schools and continuously monitoring the physical and biotic environment enabled the development of an ecological understanding of these dolphins. Continuity in these studies was provided by the fact that on each ship there was at least one experienced observer who participated during all cruise years. We present our results as an independent, research-ship based, assessment of species distributions and habitat areas.

RESULTS

Distribution and Relative Abundance of Dolphin Schools

Plots of the sighting localities of schools of spotted, spinner, striped, and common dolphins, obtained during the January-March research cruises, show the geographical distributions of these species during the northern winter season. Table 1 summarizes the numbers and sizes of the schools which were identified and studied. Geographic locations referred to in the text can be found in Figure 1.

Spotted and spinner dolphins are often in mixed schools (33.5% of spotted dolphins schools also contained spinner dolphins, Table 1), and so the sightings of spotted or of mixed spotted plus spinner dolphin schools are shown together (Fig. 3). Most of the mixed schools were encountered off southern Mexico, where the eastern form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) usually accompanied spotted dolphins (cf. Figs. 3, 4). Mixed schools were uncommon along the Equator, as was the spotted dolphin itself, especially west of long. 110°W. Large schools (>300 individuals) of spotted dolphin were widely scattered, but tended to be more common off southern Mexico. Westward extensions of distribution appeared to occur as three main lobes: about lat. 10°n, between lat. 0° and 5°N, and between lat. 2°S and 5°S.

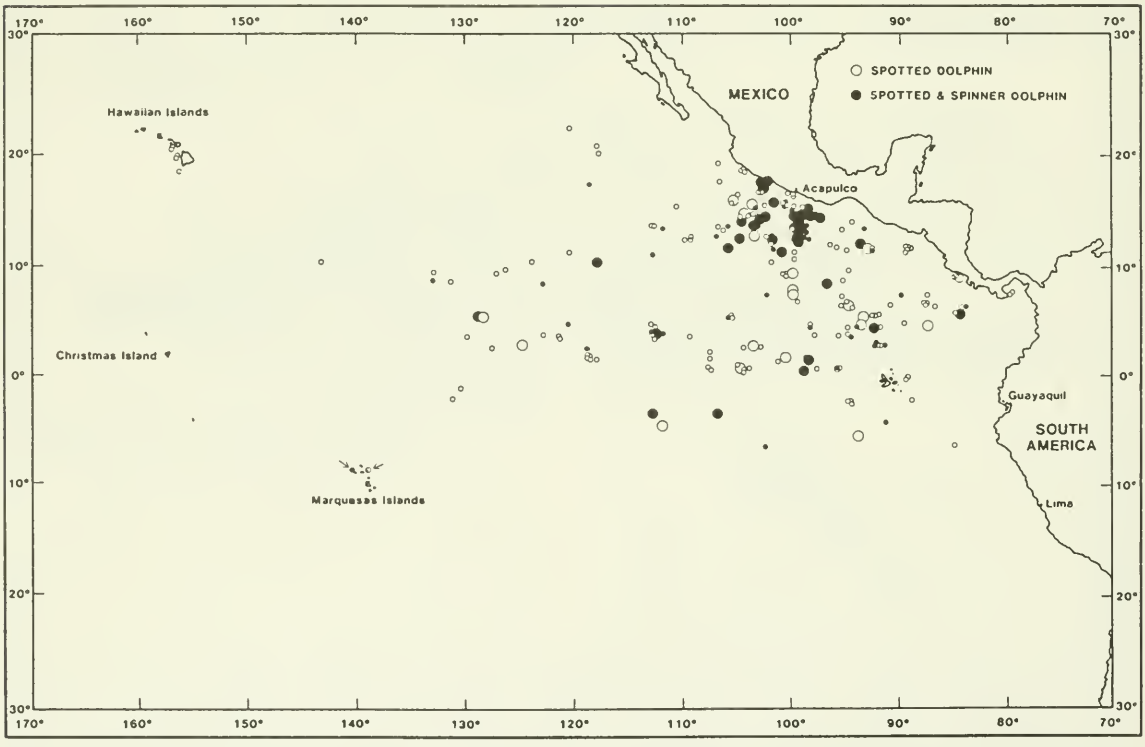

FIGURE 3.—Distribution of spotted and spotted plus spinner dolphin schools seen during the January-March research cruises. Larger circles indicate schools of >300 animals.

The spinner dolphin appears to be distributed like the spotted dolphin, with westerly extending lobes of distribution in similar latitudes (Fig. 4). Schools were infrequent along the Equator, more so than were those of spotted dolphin. The eastern spinner was encountered frequently off southern Mexico, where its main population center appeared to be relatively localized. However, eastern spinner dolphins were seen as far offshore as long. 126°W near lat. 10°N and also nearly to the Equator within a broad, 600 nmi coastal belt off Central America. The whitebelly form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) occurred in a broad range north and south of the Equator and at the southern and western portions of the total spinner dolphin range. Large schools (>300) were seen mostly off southern Mexico (eastern spinner) and south of the Equator (whitebelly spinner).

Striped and common dolphins seem to have a distribution pattern qualitatively different from that of spotted and spinner dolphins (Fig. 5). A distinct distributional lobe, consisting primarily of common dolphins, occurred off Baja California, with extensions around the Revilla Gigedo Islands (ca. lat. 19°N, long. 111°W). Between lat. 5° and 12°N, off Central America, there was a second lobe made up of both species. This lobe attenuated to the west along lat. 10°N, but appeared to re-intensify past long. 130°W. Only striped dolphins were seen in the intermediate interval between long. 100°W and 130°W along this lobe. A third lobe appeared to originate off Peru. It merged somewhat with the outer portions of the Central American lobe, and then extended westward along the Equator. Equatorial waters were frequented by both species out to about long. 100°W, beyond which striped dolphins apparently predominate. The striped dolphin is the more widespread of the two species; however, its school sizes are small (Table 1). Large schools (>300) of the common dolphin occurred within each of the three main centers of its distribution.

The above sighting data were adjusted to show the distributions of relative abundance of schools by correcting for searching effort. Effort is calculated as miles searched = time searched × ship speed. Relative abundance of schools was expressed as schools per 100 nmi searched (approximately the

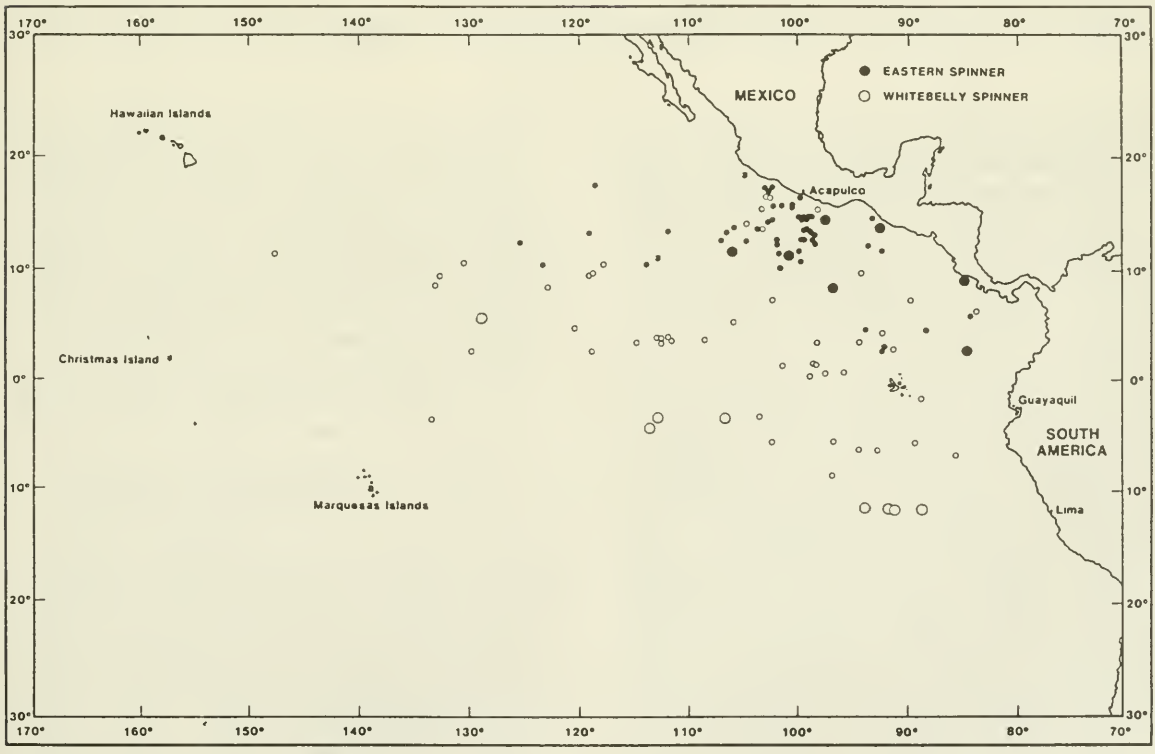

FIGURE 4.—Distribution of spinner dolphin schools, eastern and whitebelly forms, seen during the January-March research cruises. Larger circles indicate schools >300 animals.

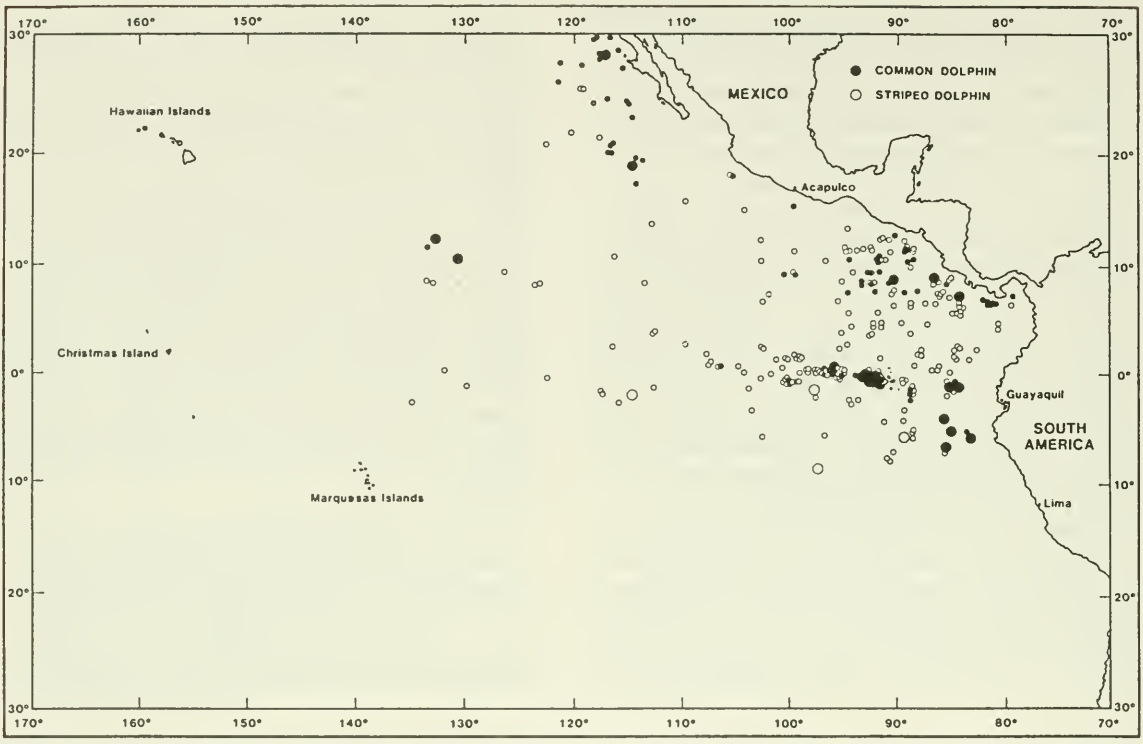

FIGURE 5.—Distribution of striped and common dolphin schools seen during the January-March research cruises. Larger circles indicate schools >300 animals.

distance searched during 1 d). Data for days during which the Beaufort wind force was equal to 4 (11-16 kn) for more than 50% of the time, or averaged more than 4, were not used. Only schools sighted at distances not more than 3 perpendicular nmi from the ship's track and not more than 5 radial nmi distant were considered, to reduce the effects due to distance on sightability. The latter criterion was not applied to the 1976 cruises, because the radial distances then were frequently overestimated. An areal smoothing procedure that consisted of calculating the average number of schools per 100 mi searched within sequential, overlapping 5° squares was employed. Sequential squares were offset 2.5° in latitude and longitude, so that each was wholly overlapped by 25% of the area of each of four adjacent squares. A day's sighting rate was assigned to a particular square if more than 50% of the search effort occurred therein, and the value was plotted at the center point of that square. If the search effort fell equally in two squares, the day's results were assigned to both squares. These moving, areal means of sightings per 100 nmi searched were plotted and contoured. Contouring (and interpolation) constituted a second level of areal smoothing.

The maps so generated describe the distribution of relative abundance of species schools as surveyed during January to March. These relative abundance data were combined for spotted and spinner dolphins and for striped and common dolphins, both because these species pairs had similar distributions and because pooling gave desirable sample sizes.

The combined spotted and spinner dolphin map (Fig. 6) shows some patterns already noted from the school distribution. These schools appeared relatively more abundant off southern Mexico (mostly spotted and eastern spinner dolphins) and again along an east-west band just north of the Equator, especially west of long. 105°W. Another band of greater abundance occurred south of the Equator. Spotted and spinner dolphins appeared less abundant just west of Costa Rica, off the coast of northern South America, and along the Equator. A weak lobe of higher relative abundance extended west of long. 120°W broadly about lat. 10°N.

Striped and common dolphins show a relative abundance pattern in which areas of higher density tend to be complementary to that of spotted and

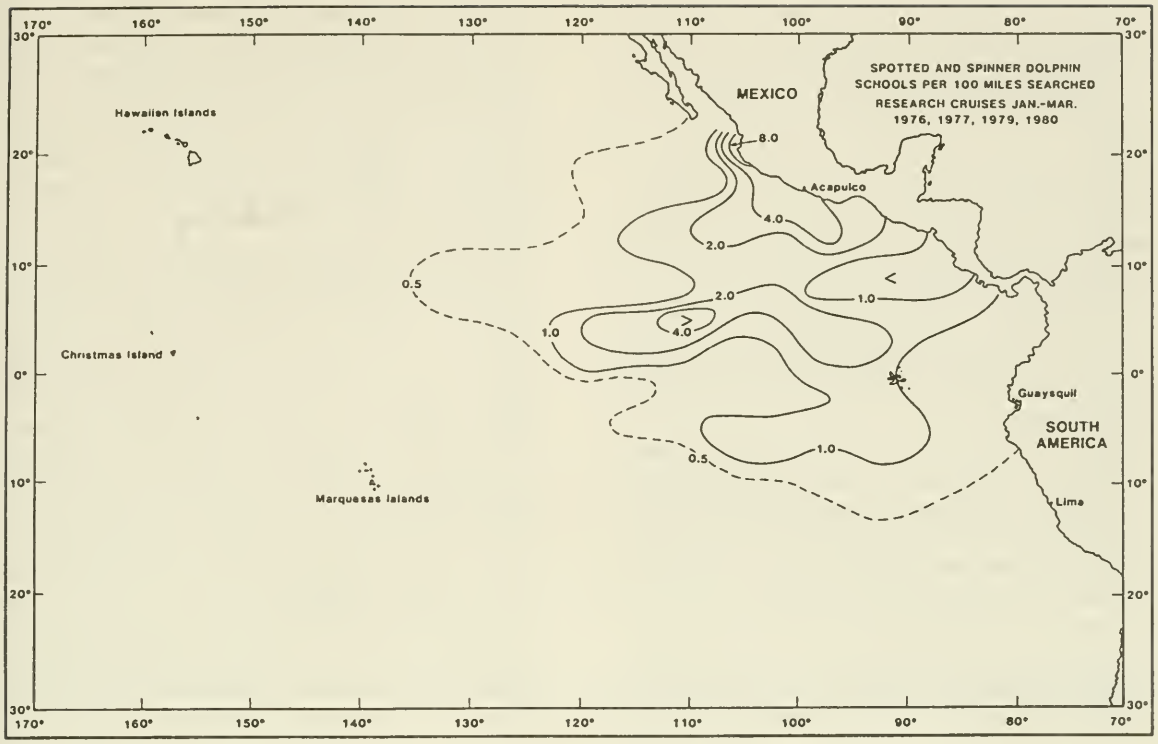

FIGURE 6.—Distribution of relative abundance of spotted and spinner dolphins, inferred from data of the January-March research cruises. Hawaiian and Marquesan sightings are not considered.

spinner dolphins (Fig. 7). Conspicuous lobes extended from off Baja California and also broadly from the coasts of Central America and northern South America out to and along the Equator. Within the latter lobe, centers of higher relative abundance occurred west of Nicaragua and Costa Rica and west of the Galapagos Islands, all areas where reduced abundance of spotted and spinner dolphins occurred. The Galapagos area and the lobe off Baja California were dominated by the common dolphin (cf. Fig. 5).

Dolphins of Tropical Water and Upwelling-Modified Water Habitats

The areas of greater frequency of spotted and spinner dolphins during January-March are the typical tropical waters of the eastern tropical Pacific. These waters are underlain by a sharp thermocline, generally >2°C/10 m, at depths usually much <50 m. The surface temperatures are >25°C, and the salinities <34‰. Such tropical waters are defined by Wyrtki (1966, 1967) as Tropical Surface Water (see Fig. 1). In particular the warm "Inner Tropical" Waters (Wyrtki 1964a) lying primarily north of the Equator comprise the major habitat of spotted and spinner dolphins (Fig. 6). The waters south of the Equator, where the relative abundance of these dolphins is also higher, are seasonally tropical, and are therefore called southern Subtropical Surface Water (Wyrtki 1966, 1967). These waters, occurring approximately south of lat. 2.5°S, have surface salinities >35‰, and during January-March (southern summer), warm to more than 26°C over a shallow, sharp thermocline. Since spotted and spinner dolphins occur there frequently, at least during January-March, it appears that spotted and spinner dolphins prefer all waters whose characteristics are, or become, tropical in the eastern Pacific. However the primary habitat appears to be the "Inner" Tropical Waters north of the Equator.

In contrast striped and common dolphins appear to prefer waters with more variable conditions during January-March. Their most important habitat appears to be broadly centered about equatorial waters (Fig. 7). This band of distribution extends into the central Pacific along the Equator. In the east it broadens widely to include Tropical Water off Cen-

tral America and Subtropical Water off Peru. The equatorial distribution is in Equatorial Surface Water (Wyrtki 1966, 1967), a transitional water mass straddling the Equator and characterized by salinities between 34 and 35‰, upwelling, and a relatively weak thermocline. These waters are markedly cooled from June to December (southern winter-spring) by increased upwelling and by advection from the Peru Current. In the Subtropical Water habitats of striped and common dolphins, both off Peru and Baja California, there are also large seasonal changes in temperature structure and effects from upwelling. Finally the Tropical Water habitat in the Central American Bight is notably variable (below).

The waters we call the "Central American Bight" (roughly, the near coastal waters from Guatemala to Ecuador) constitute the most important area of overlap for spotted, spinner, striped, and common dolphins, but this overlap is not balanced among the species. These waters are tropical, but they are the most variable within the Tropical Surface Water province. The Equatorial Countercurrent, flowing eastward between lat. 4°N and 10°N, terminates and turns there, creating a complex circulation. The annual north-south migration in these latitudes of the Intertropical Convergence Zone, where north and south trade winds meet, bring southerly winds, rain, reduced salinity, and an intensified Countercurrent during the second half of the year (Bennett 1966; Wyrtki 1967, 1974; Forsebergh 1969). Later during the northern winter (January-March), northeasterly winds blow across Central America from the Atlantic, producing coastal upwelling, wind stirring, and more complex temperature patterns. The Costa Rica Dome, a localized, offshore upwelling at about lat. 8°N, long. 90°W (Wyrtki 1964b), also may be seasonally intensified (Hofmann et al. 1981).

These variable Central American Bight waters appear to have more abundant schools of striped and common dolphins than of spotted and spinner dolphins (cf. Figs. 3-7). It seems that all areas with greater concentration of striped and common dolphins have highly variable oceanographic features that are "upwelling-modified".

In spite of the rather strong overlap in distribution among the four dolphin species in the Central America Bight, the biogeographic distinction, including the relationships to environment, between

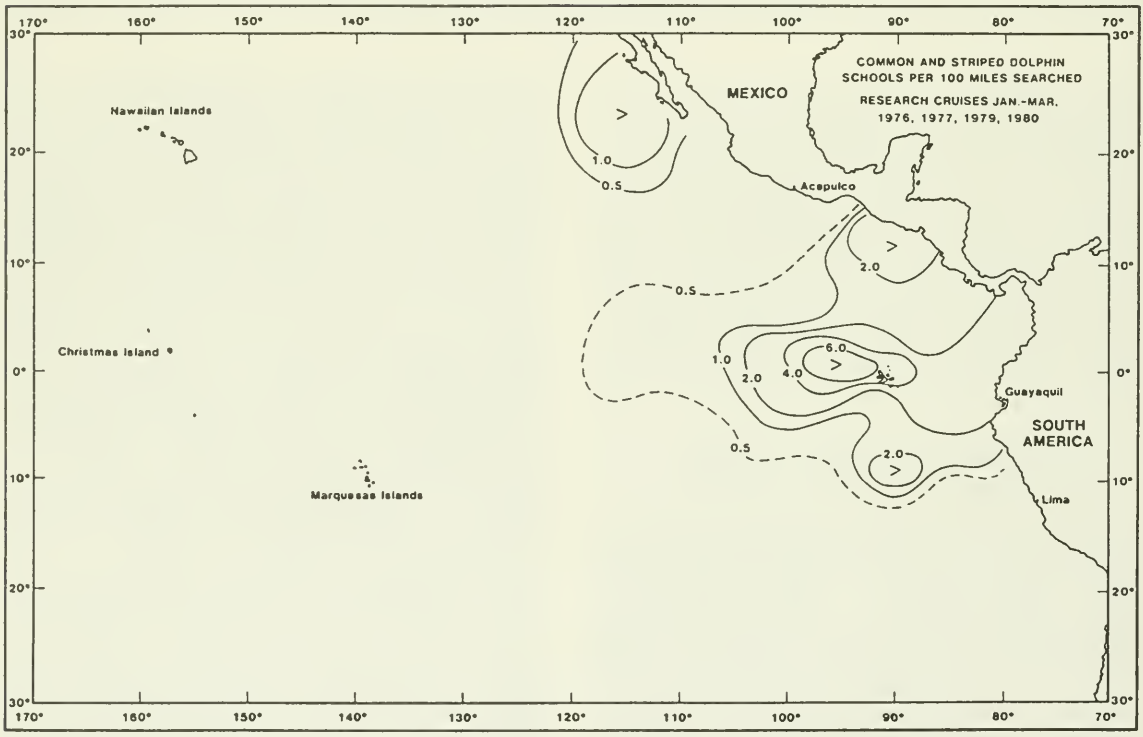

FIGURE 7.—Distribution of relative abundance of striped and common dolphins, inferred from data of the January-March research cruises.

the spotted and spinner dolphins of the Tropical Water and the striped and common dolphins of the Upwelling-Modified Water may be quite apparent. This was the case during the intensive winter surveys of 1979 in the Central American Bight, shown in Figure 8. Superimposed in the figure are contours of the 20°C isotherm depth (essentially the thermocline depth) which were obtained from expendable bathythermograph probes dropped at 30-60 mi intervals (55.6-111.1 km). Notice that spotted and spinner dolphins were encountered mainly off southern Mexico, where the deeper 20°C isotherms indicated the occurrence of a large surface lens of warm water. The warmest surface waters in the eastern tropical Pacific normally occur in this area; the thermocline gradient is weaker, and the annual variation in surface temperature is relatively small (Wyrtki 1964a). In the more variable tropical waters of the Central American Bight, where the thermocline had shoaled or ridged to <60 m, both these species were seen too. However, striped and common dolphin schools predominated, especially near the shallower isotherms that mark the location of the Costa Rica Dome. Finally the equatorial distribution of primarily striped and common dolphins was evident. The sampling suggested that Subtropical Waters south of the Galapagos Islands were probably also important to these latter two species. A 1977 aerial survey of cetaceans in these waters off Central America (SWFC 1977[3]) obtained results similar to those just described.

Though there appear to be large-scale geographic differences in the habitats of spotted and spinner dolphins and of striped and common dolphins, there was no evidence of negative association among these species. The frequency of days in the Central American Bight, both in 1979 and 1980, with different combinations of these species encountered, are summarized in Table 2. There was no evidence, using chi-square contingency tests for association among spotted and/or spinner dolphins and striped or common dolphins, that the species were not occurring independently on any particular day.

Our contention that spotted and spinner dolphins and striped and common dolphins differentially inhabit waters of different oceanographic characteris-

[3]Southwest Fisheries Center (SWFC). 1977. Aerial survey trip report January - June 1977. Admin. Rep. No. LJ-78-01, 73 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

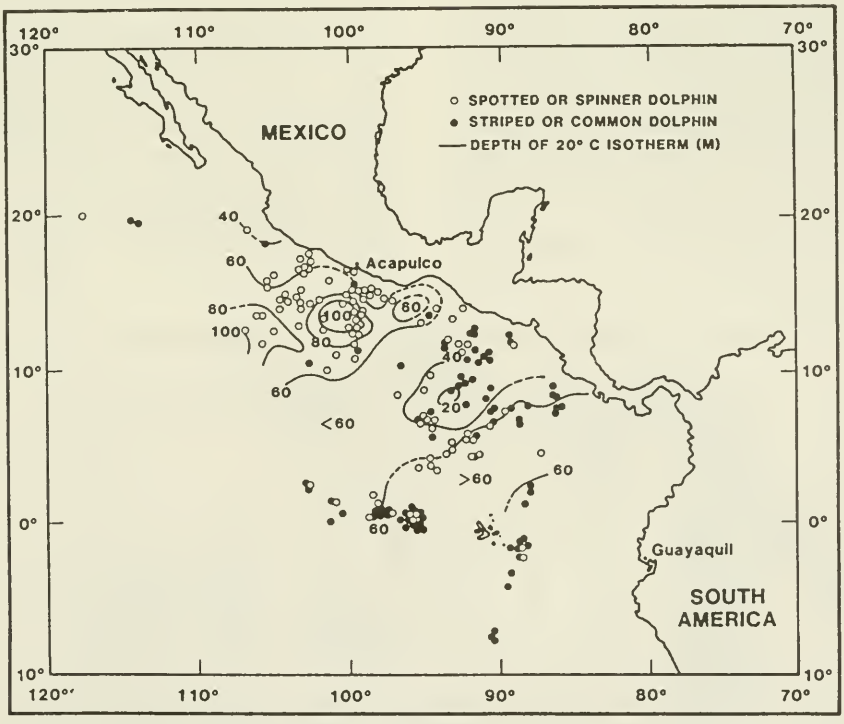

FIGURE 8.—Distribution of dolphin schools by species type in the Central American Bight, with reference to the depth of the 20°C isotherm. Data are from the January-March cruises of 1979.

TABLE 2.—Number of days according to combinations of four species of dolphins that were encountered in the Central American Bight.

		Spotted and/or spinner				Striped		Common	
Year	Area[1]	Alone	With striped	With common	With striped + common	Alone	With common	Alone	None of these spp.
1979	N	17	2	0	0	1	1	1	6
	S	6	7	0	4	6	1	6	8
1980	N	9	2	0	0	0	0	0	0
	S	5	5	1	4	6	3	3	7

[1]Northern (N) and southern (S) areas are partitioned to illustrate species differences by area; the dividing line is perpendicular to the coast at lat. 16°N.

tics is supported by physical environmental measurements. The data indicated a species differential with respect to waters with temperature ≥25°C and salinities ≤34.5‰, and waters of <25°C and >34.5‰. The former is primarily Tropical Surface Water and the latter primarily Equatorial-Subtropical Surface Water. Of 217 spotted and/or spinner dolphin schools encountered during the January-March cruises, and having associated temperature and salinity measurements, 80.6% were in this Tropical Surface Water, while only 19.4% were in the Equatorial-Subtropical Surface Water. In comparison 53.7% of 229 similarly observed schools of striped and/or common dolphins were in the Tropical Surface Water and 46.3% were in the Equatorial-Subtropical Water. The differential in percentages by species pair reflects the more uniform "Inner Tropical" Surface Water habitat of spotted and spinner dolphins and the importance to striped and common dolphins of both the variable Tropical Water off Central America and the variable waters along the Equator, west of Peru, and southwest of Baja California.

Because the school sighting data are represented by many combinations of temperature and salinity from various areas, it is useful to summarize these results in terms of an integrated measure of temperature and salinity, i.e., sigma-*t*, a measure of water density (see Sverdrup et al. 1942). Table 3 lists the numbers and percentages of spotted and spinner and of striped and common dolphins according to their occurrence at different intervals of sigma-*t*. The percentages of striped and common dolphin schools were higher than that of spotted and spinner dolphin schools for sigma-*t* ≥22.5 (primarily Equatorial-Subtropical Water). The opposite was true for sigma-*t* <22.5 (primarily Tropical Water). The difference in percentage distribution by species pair is significant ($P < 0.01$, Kolmogorov-Smirnov test).

Seasonal Features of Habitats

It is not clear how dolphin populations are affected by seasonal changes in the environment, although the available data suggest what may happen. The far offshore habitat of spotted and spinner dolphins, between long. 120°W and 140°W at about lat. 10°N, is an important "porpoise-tuna" fishing area during

TABLE 3.—Percent distribution of dolphin schools[1] according to surface water density (sigma-*t*).

sigma-*t*	Spotted	Spinner[2]	Total	%	Striped	Common	Total	%
+18.5-19.0					2		2	0.9
+19.0-19.5	2	1	3	1.4	5		5	2.2
+19.5-20.0	6		6	2.8	8		8	3.5
+20.0-20.5				0.0	2	1	3	1.3
+20.5-21.0	5	2	7	3.2	6	2	8	3.5
+21.0-21.5	16	12	28	12.9	11	2	13	5.7
+21.5-22.0	43	28	71	32.7	27	6	33	14.4
+22.0-22.5	12	32	54	24.9	26	19	45	19.7
+22.5-23.0	15	6	21	9.7	22	8	30	13.1
+23.0-23.5	8	11	19	8.8	39	15	54	23.6
+23.5-24.0	2	4	6	2.8	10	3	13	5.7
+24.0-24.5	2		2	0.9	6	6	12	5.2
+24.5-25.0					1	2	3	1.3
+25.0-25.5								
Total	111	96	217	100	165	64	229	100

[1]January-March, research cruises, 1976, 1977, 1979, 1980.
[2]Includes mixed spinner + spotted dolphin schools.

the spring and summer months (Calkins 1975). However there is little information from that area during the winter months (when there is little fishing), except for results from the January-March research cruises, which indicated that population densities there were not high (Fig. 6). This suggests a summer buildup in the concentration of these dolphins. This is likely because the offshore habitat is centered close to or along the divergence zone at the northern boundary of the North Equatorial Countercurrent, where the thermocline ridges and biological production is increased (Cromwell 1958). During the northern summer, the trade winds over the offshore habitat abate, ridging intensifies (Wyrtki 1964a, 1974), and porpoise-tuna fishing expands west of Clipperton Island (at ca. lat. 10°N, long. 109°W). The increase in fishing may be due to better weather, but possibly also to an increased abundance of dolphins and tuna.

The seasonal change in environment of the eastern tropical Pacific most likely to affect the distribution of dolphins is that due to the movement of the southern border of the tropical waters. During the northern winter, tropical conditions usually extend to about 15° south of the Galapagos Islands, when a shallow surface layer of warm water develops over what is actually Subtropical Water. During the northern summer, the cool Peru and South Equatorial Current strengthen, and a conspicuous thermal front, marking the southern boundary of Tropical Surface Water, usually develops. This Equatorial Front (Wyrtki 1966) is located a few degrees north of the Equator except for a short section east of the Galapagos Islands.

We studied the relationship of the Equatorial Front to dolphin populations during an October-November 1977 cruise of the *David Starr Jordan*. The Equatorial Front was conspicuous, as were the effects of the cool Peru and South Equatorial Currents (Fig. 9). Only 4 of 27 sightings of spotted and spinner dolphins schools in the equatorial region occurred in the cool, Equatorial and Subtropical Waters south of the front. The majority of the remaining 23 sightings were along the Equatorial Front, at the southern border to the warm Tropical Surface Water. These same species had occurred throughout these southern waters during January to March (Figs. 3, 4), when sea surface temperatures of 25°C or more prevailed over this entire area. The apparent redistribution of dolphin schools along the warm edge of the Peru Current and Equatorial Front appeared to be restricted to the spotted and spinner species, suggesting their seasonal movements away from cool southern waters. By implication these same dolphin species may migrate into southern waters during the warm season. Seasonal movements of dolphins (unidentified) in the southern waters is also suggested by results from the 1967 and 1968 EASTROPAC cruises (Love 1971, 1972). On the other hand, we did see during the October-November cruise four schools of spotted and spinner dolphins in cool Subtropical Water, and observers aboard tuna seiners have also reported these same species there during the cool season.

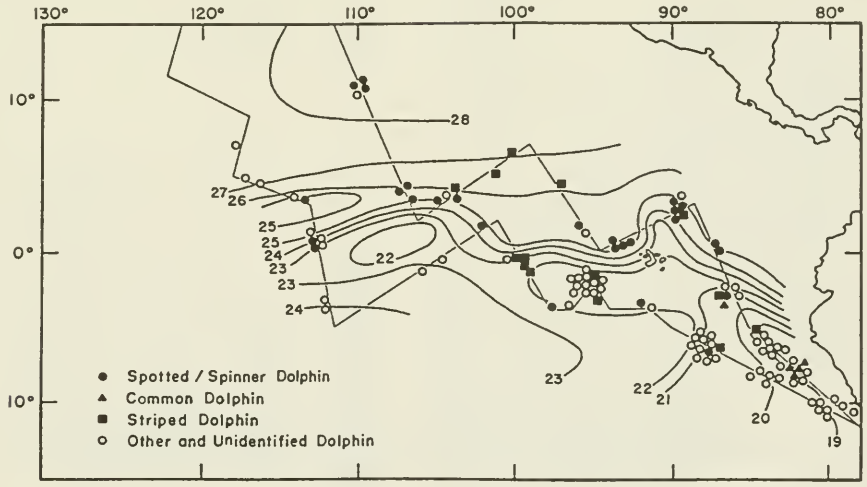

FIGURE 9.—Distribution of dolphin schools in the equatorial region during October-November 1977, relative to surface isotherms (°C). Notice the Equatorial Front or zone of rapid temperature change just north of the Equator. Clumping of sightings along the track is due to nighttime travel by ship. "Other" dolphins are primarily pilot whales.

Dolphin Communities

The habitat differences discussed also apply to other delphinid species, so that there seem to be different communities of dolphins in the eastern Pacific. To show how the cetacean communities differ between the habitats dominated by spotted and spinner and by striped and common dolphins, the eastern Pacific was divided into Areas I and II (Fig. 10, inset) that separate the main habitat areas of these two species pairs. Area I is primarily Tropical Surface Water and includes most areas where thermocline ridging is a dominant physical feature. Area II is primarily Equatorial-southern Subtropical Surface Water, but also includes the wedge-shaped area of variable Tropical Water in the Central American Bight. Area II comprises most of the waters we have called Upwelling-Modified.

In each of these two areas, only schools sighted at ≤1.0 nmi perpendicular to the ship's tracks were listed. This requirement was imposed so that percent species composition could be based on species schools, that to the largest practical degree, could all be sighted with equal probability, if present. The change in "sightability" with distance is different for each species because of differences in behavior, coloration, size, etc.

Our data indicate that the species composition of delphinids is different in these two areas. Percentage composition was determined for spotted; spinner; striped; common; bottlenose, *Tursiops truncatus*; rough-toothed, *Steno bredanensis*; and Risso's, *Grampus griseus*, dolphins, and for "blackfish", *Peponocephala electra/Feresa attenuata*; pilot whales, *Globicephala macrorhynchus*; and others (Table 4). Among 8 of 10 species-groups specifically identified in Table 4, there were significantly higher percentages of spotted, spinner, and rough-toothed dolphin schools in Area I than in Area II (Fig. 10). Risso's and bottlenose dolphins were important species in both areas, and their percentage values did not differ significantly between the areas. The percentages due to striped and common dolphins and pilot whales increased in Area II relative to Area I. Though reduced, the spotted dolphin remained important in the Area II dolphin community. The increase in percent composition of the common dolphin in Area II was not quite significant, reflecting the inclusion in Area I of that species' distributional lobe off Baja California. Overall, the species composition differed significantly between the two areas, as determined by chi-square contingency test of the frequency of species other than spotted, spinner, striped, and common, i.e., the species not initially considered when delimiting Areas I and II ($\chi^2 = 74.4$, df = 5, $P < 0.005$).

Additional evidence for the distinctiveness of the equatorial and subtropical portions of the Area II community is provided by observations along equatorial transects and transects south and south-

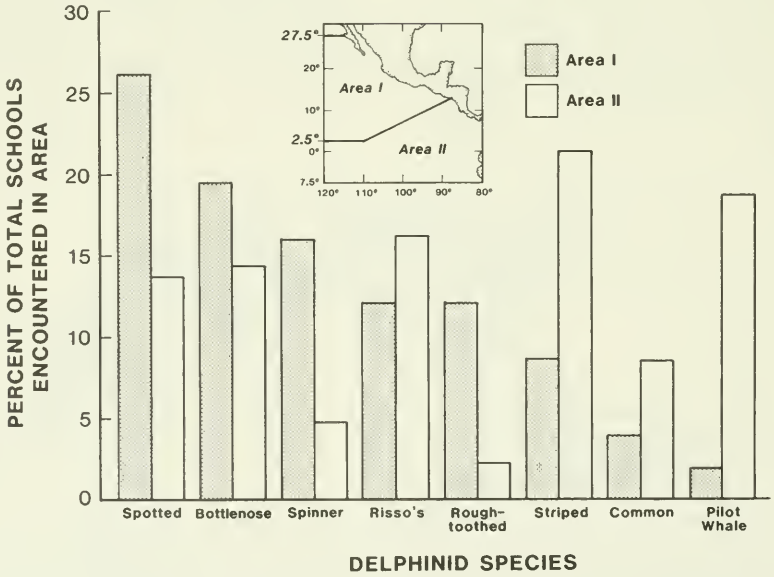

FIGURE 10.—Percent species composition of some important cetaceans, by Area I and II. See Table 4.

TABLE 4.—Percent composition of species as encountered in two areas[1] during the January-March research cruises.

Delphinid spp.[2]	Area I Schools	%	95%[3] C.I.	Area II Schools	%	95%[3] C.I.
Spotted, *Stenella attenuata*	67	24.7	19.6-29.8	55	13.2	10.0-16.4
Spinner, *Stenella longirostris*	41	15.1	10.8-19.4	19	4.6	2.6-6.6
Striped, *Stenella coeruleoalba*	22	8.1	4.9-11.3	86	20.6	16.7-24.5
Common, *Delphinus delphis*	10	3.7	1.5-5.9	34	8.2	5.6-10.8
Pilot whale, *Globicephala macrorhynchus*	5	1.8	0.2-3.4	75	18.0	14.3-21.7
Risso's, *Grampus griseus*	31	11.4	7.6-15.2	65	15.6	12.1-19.5
Bottlenose, *Tursiops truncatus*	50	18.5	13.9-23.1	58	13.9	10.6-17.2
Rough-toothed, *Steno bredanensis*	31	11.4	7.6-15.2	10	2.4	0.9-3.9
"Blackfish", *Peponocephala electra* or *Feresa attenuata*	8	3.0	1.0-5.0	1	0.2	0-0.6
Other	6	2.2	0.2-4.2	14	3.4	1.7-5.1
Total	271			417		

[1]Areas are shown in Figure 10.
[2]Species in mixed schools were tabulated separately.
[3]Normal approximation to binomial distribution.

east of the Galapagos Islands, i.e., off Peru. Unlike during the January-March cruises, physical oceanography was the primary task on most of these transects, hence the ships did not usually divert course toward the schools, and many schools could not be identified. Nevertheless some idea of the species compositions can be obtained. The observations (Table 5) showed that pilot whales and Risso's and bottlenose dolphins were frequently encountered species during October-December off Peru, and common dolphins were often seen near the coast. On the equatorial transects, between long. 85°W and 110°W, striped and common dolphins were the characteristic species. The common dolphin was seen most often near the Galapagos Islands. Pilot whales were relatively abundant during May-July 1981 in this equatorial section. West of long. 110°W along the Equator, pilot whales again were the most frequently encountered species. Interestingly, sightings of Fraser's dolphins, *Lagenodelphis hosei*, and "blackfish" (probably *Peponocephala electra*) were also relatively frequent, especially between long. 110°W and 145°W. These two species often school together and appear to prefer equatorial waters (Perryman et al.[4]). In the next section, another distinctive feature of equatorial waters will be brought out.

Dolphins, Birds, and Tuna

A conspicuous feature distinguishing the dolphin communities is the difference in the species-specific association with tunas. In the eastern tropical Pacific, spinner dolphins and especially spotted dolphins are found associated with "surface" yellowfin tuna. It is these two species, therefore, that are mainly affected by the porpoise-tuna fishery (Smith 1983). Surface tunas occur at the sea surface and can be caught by purse seine, trolling, and pole-and-line gear. "Deep tunas" of the same species are caught by longline gear, generally in and below the thermocline. Since these surface tunas drive food to the surface, making it available to certain seabirds (Ashmole and Ashmole 1957; Murphy and Shomura 1972), a reliable indication that tuna are accompanying a dolphin school is the presence of a bird flock. Birds are the most important cue used by fishermen to locate dolphin-tuna schools.

Birds do not occur equally among the different dolphin species. During the 1977, 1979, and 1980 January-March cruises (when the best bird observa-

[4]Perryman, W. F., D. W. K. Au, and S. Leatherwood. Manuscr. prep. Melon-headed whale, *Peponocephala electra* (Gray, 1946) (with notes on the pygmy killer whale *Feresa attenuata*). Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 5.—Number of schools for species seen along equatorial and southeastern Pacific transects.

Dolphin spp.	Region:	Off Peru: 0-10°S, 83°-95°W		Equator: 2°N-2°S 85°-110°W			Equator: 2°N-2°S 110°-145°W		Equator: 2°N-2°S 145°-180°W
	Ships:	*D. S. Jordan*	*Researcher*	Ocean-*ographer*	*Researcher*	*Reseacher*	Ocean-*ographer*	Ocean-*ographer*	Ocean-*ographer*
	Dates:	Oct.-Nov. 1977	Oct.-Dec. 1981	May-July 1981	July-Sept. 1980	Oct-Dec. 1981	Mar.-Apr. 1980	May-July 1981	Mar.-Apr. 1980
Unidentified		7	13	34	20	29	22	8	1
Spotted, *Stenella attenuata*		3	1	3	3		2	2	1
Spinner, *S. longirostris*		3		1	2		1	1	1
Striped, *S. coeruleoalba*		5	1	14	13	11	3	3	1
Common, *Delphinus delphis*		4	6	18	9	13			
Bottlenose, *Tursiops truncatus*		10	15	5	4	1		1	
Pilot, *Globicephala macrorhynchus*		14	9	14	4	3	16	5	7
Risso's, *Grampus griseus*		23	14	2		1	7		1
Rough-toothed, *Steno bredanensis*		1		1		1	4		1
Fraser's, *Lagenodelphis hosei*							7	1	1
"Blackfish", *Peponocephala electra* or *Feresa attenuata*		2		1			8		2
False killer whale, *Pseudorca crassidens*		1				1	1		2
Killer whale, *Orsinus orca*		1	1	1	2	3			

tions were taken), 70.7% of 167 spotted, spinner, or mixed spotted and spinner dolphin schools, sighted between lat. 5°N and 30°N (where most dolphin-tuna associations occur), had 10 or more associated birds (Table 6). We assume this minimum flock size indicates associated tuna, although we did not often actually see the tuna. For the same period and area, 30.6% of 49 common dolphin schools and only 1.6% of 64 striped dolphin schools were with 10 or more birds. The different percent occurrences indicate that tuna are most frequently associated with spotted and spinner dolphins and very seldom with the striped dolphin.

The bird species most numerous in offshore waters with dolphin schools are boobies (*Sula* spp.); wedge-tailed shearwaters, *Puffinus pacificus*; and sooty terns, *Sterna fuscata*. Frigate birds (*Fregata* spp.) are also closely associated with these dolphins, though their average flock size is only seven (Au and Pitman[5]). These bird species are all strongly dependent upon tunas in their feeding. Our observations are that the birds feed primarily in association with the fish, not the dolphins.

The dolphin-tuna-bird association appears to be area- as well as species-specific. Assuming flocks of ≥10 birds indicate the presence of yellowfin tuna, this association seems to occur in all areas with higher relative abundance of spotted and spinner dolphins (Fig. 11). The association seldom occurs along the Equator, or in areas outside the traditional porpoise-tuna fishing grounds (roughly these are waters within the triangular-shaped area whose base is formed by the American coasts between lat. 25°N and 15°S, and whose apex is at lat. 10°N, long. 150°W; see Calkins 1975 and IATTC 1979-81), even though the required species of dolphins, tuna, and birds may be present there. Relatively few of the spotted or spinner dolphin schools sighted near the Equator were with bird flocks. South of the Equator and in the Central Pacific, there are abundant flocks of sooty terns with fish schools, but dolphins do not usually co-occur (Au and Pitman fn. 5). The most important area of the dolphin-tuna-bird association is centered about the divergence zone near lat. 10°N, an important porpoise-tuna fishing ground for yellowfin tuna (primarily Area I of Figure 10).

These areal changes in the interactions among species are usually clearly apparent during north-south transects across the eastern Pacific during any season. An example is the July-September 1980, NOAA ship *Researcher* transits between Manzanillo, Mexico, and lat. 3°S, long. 100°W, via Clipperton Island. At that time Tropical Surface Water (T > 25°C) extended to the Equator with transition toward Equatorial Water marked by temperature and salinity fronts at lat. 5°N-6°N and at the Equator (Fig. 12). In the tropical waters north of the front at lat. 5°N there was a conspicuous increase in abundance of flocks of sooty terns, boobies, and shearwaters (*Puffinus* spp.), all broadly centered about the thermocline ridge at lat. 10°N. The larger gadfly petrels (*Pterodroma* spp.) were also abundant. All of these birds frequently flock over fish and dolphins. South of this boundary was another avian group, with *Pterodroma leucoptera*, a small petrel from the Southern Hemisphere, and planktivorous storm petrels (*Oceanodroma* spp.) predominating, and peak abundances at the Equator. These latter birds usually feed independently of fish and seldom flock over fish and dolphins.

Correlations among water masses, seabirds, and the different cetaceans along the transect were difficult to quantify because of the small sample size of the latter. However, the observations are supportive of such relationships. There were 39 dolphin schools, of which 15 were unidentified, and 21 whale schools along this transect. Spotted and spinner

[5]Au, D. W. K., and R. L. Pitman. Manuscr. prep. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 6.—Dolphin schools associated with seabirds.

	5°N-30°N			<5°N		
Dolphin spp.	Schools	with ≥10 birds	%	Schools	with ≥10 birds	%
Spotted	95	56	58.9	40	8	20.0
Spotted and spinner	55	53	96.4	21	8	38.1
Spinner	17	9	52.9	19	6	31.6
Common	49	15	30.6	10	1	10.0
Striped	64	1	1.6	76	1	1.3
Rough-toothed	40	5	12.5	13	1	7.7
Other/unidentified	388	17	4.4	189	6	3.2

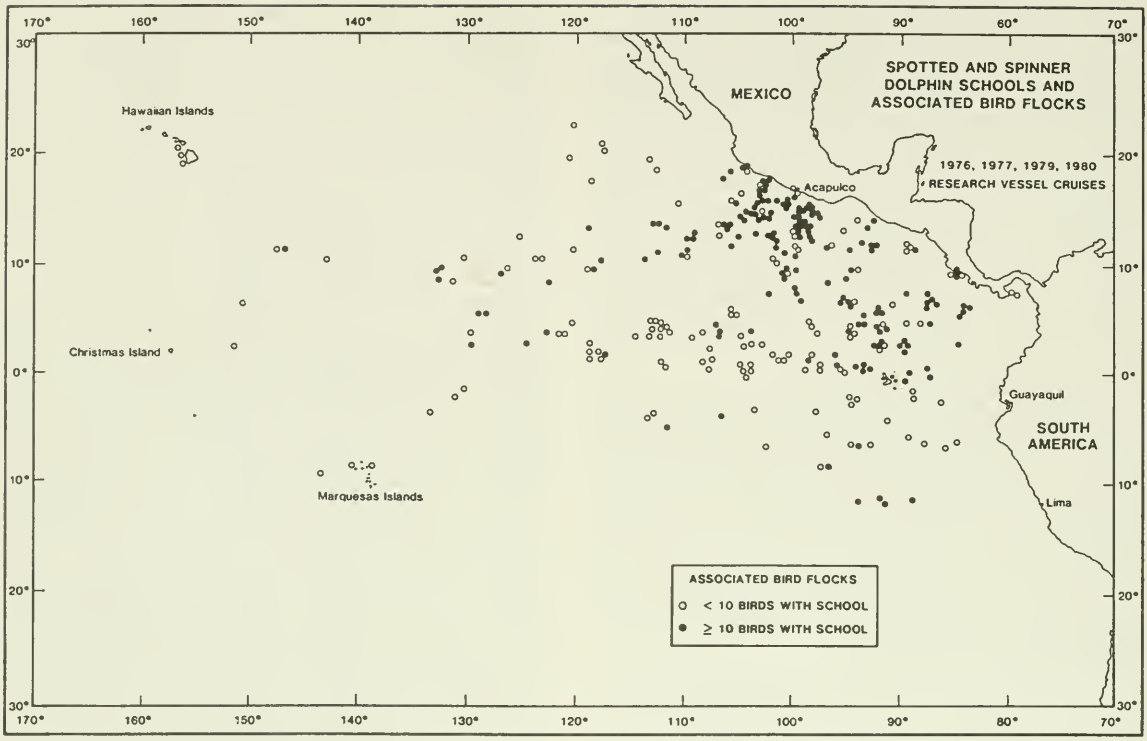

FIGURE 11.—Distribution of bird-associated spotted and spinner dolphin schools during the January-March research cruises. Schools with 10 or more birds are assumed to be with tuna.

dolphns did occur coincidentally with bird flocks (and probably with tuna) in the warmer tropical waters centered about lat. 10°N, but also were seen at the Equator, though without associated bird flocks. Striped and common dolphins occurred in coastal and equatorial waters, without bird flocks. These latter dolphins were the characteristic species on the equatorial transect of this same cruise (see Table 5, col. 4), where only one of the schools seen, a mixed spotted and spinner dolphin school, had an associated bird flock. The distinct change in the bird fauna south of lat. 5°N to species that do not forage commensally with fish suggests there are changes with water masses in the nature of epipelagic prey and how the top predators forage.

DISCUSSION

It should not be surprising that the two major divergence zones of the eastern Pacific, near lat. 10°N and along the Equator, are important features of the oceanic habitats of eastern Pacific cetaceans. Enriched by the effects of wind and the major zonal currents (Brandhorst 1958; Cromwell 1958; Reid 1962; Wyrtki 1966), the zones are evident areas of enhanced biological production (Blackburn 1966, 1976; Blackburn et al. 1970; King 1974; Parsons et al. 1977; Brinton 1979). that are important to tunas (Calkins 1975; Blackburn 1965; Blackburn and Laurs 1972; Blackburn and Williams 1975; Sund 1981) and cetaceans as discussed above. These two zones are not qualitatively the same, however; the strong, shallow thermoclines that have been related to successful porpoise-tuna fishing (Green 1967; Miller et al.[6]) and to aggregations of dolphins and baleen whales (Rovnin 1969; Volkov and Moroz 1976) are characteristic of the lat. 10°N zone, but not of the Equator. Similarly the oxygen minimum layer, noted by Perrin et al. (1976) to be correlated with the distribution of the spotted dolphin, occurs only north and south of the Equator in the eastern Pacific. Equatorial waters are characterized by shallow, weak (<2°C/10 m) thermoclines, due to upwelling and the Equatorial Undercurrent, and cool surface temper-

[6]Miller, F. R., C. J. Orange, R. H. Evans, and K. A. Bliss. Manuscr. prep. Analysis of environment related to tuna fishing in ETP. Inter-American Tropical Tuna Commission, La Jolla, CA 92038.

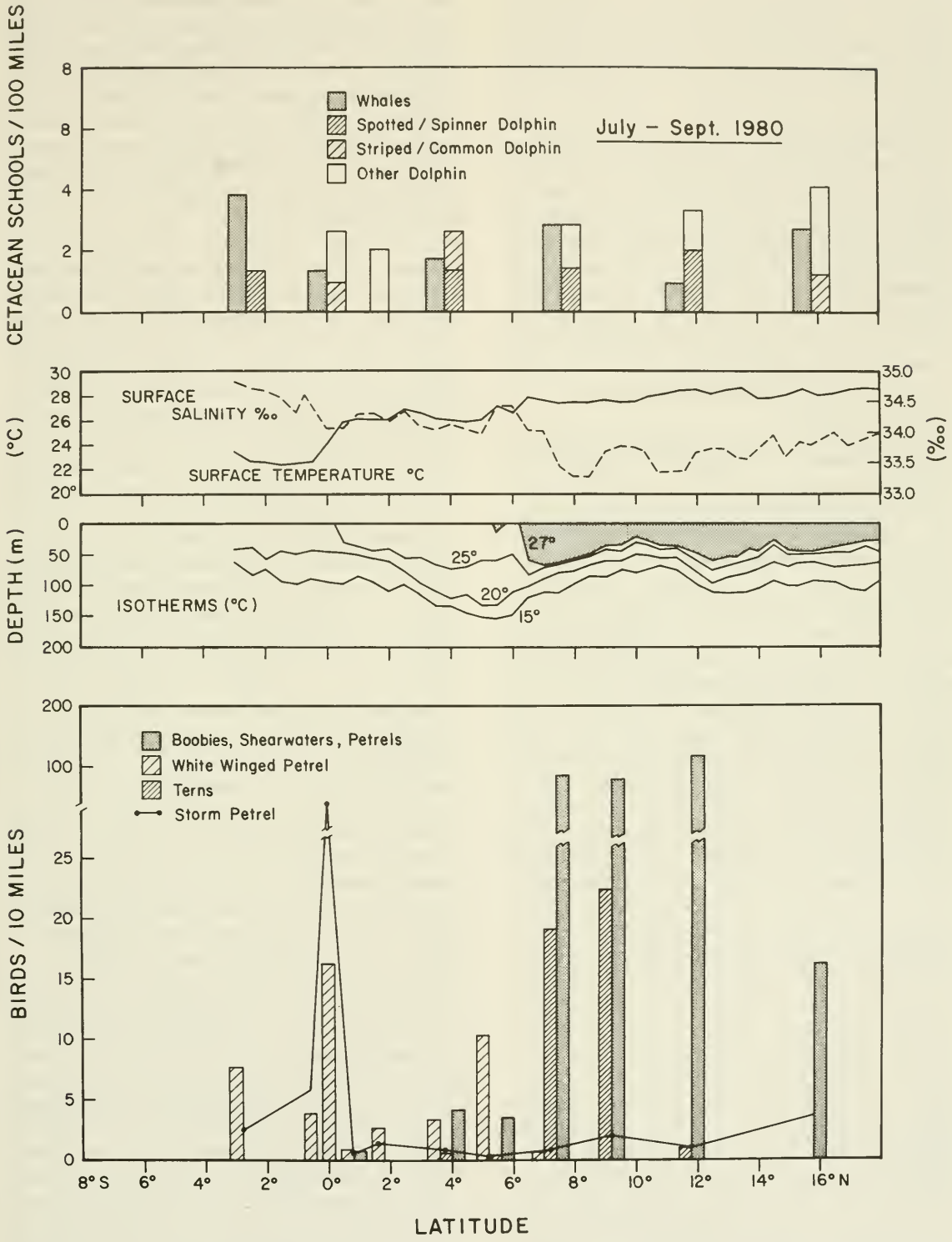

FIGURE 12.—Transect along long. 110°W, July-September 1980, showing changes in cetaceans, birds, and temperature and salinity. The relative abundance of dolphin schools include unidentified schools which were prorated according to species ratios of identified schools.

ature from June through December. These waters support a different cetacean community (Table 5), though school densities there can be as high as in areas off Mexico and Central America (Au et al. 1980).

Other relationships between distribution and movements of dolphins and water masses, convergences, and thermal conditions have been described by Fraser (1934), Gaskin (1968), Kasuya (1971), Nishiwaki (1975), Evans (1975), and Miyazaki and Nishiwaki (1978). Hui (1979) found that common dolphins off California tended to occur over prominent features of bottom topography. The deep depths of such areas suggest that surface eddies and convergences caused by topography-induced accelerations to deep reaching currents (Sverdrup et al. 1942; Neumann 1960) may have concentrated food and attracted the dolphins.

The distributions of dolphin species as seen from the January-March cruises (Figs. 3-7) are similar to the all-season school distributions derived from data of scientific observers aboard tuna seiners. These data, consisting of thousands of sightings per species, were recently summarized by Scott (1981) and Perrin et al. (1983). The same major distributional patterns as presented here for the January-March cruises were apparent, including, for spotted and spinner dolphins, the relative unimportance of equatorial latitudes and the secondary band of increased concentration of schools 2°-5° north of the Equator. The latter may be related to the Equatorial Front and increased food concentration and possibly production in the convergence zone there (Sette 1955; King and Iverson 1962; Blackburn and Laurs 1972; Murphy and Shomura 1972; Pak and Zaneveld 1974; Blackburn and Williams 1975; Greenblatt 1979). Increased abundance of micronekton occurs at least sometime in this zone (Love 1971, 1972; Blackburn and Laurs 1972). The purse seiner data, like those of this paper also showed spotted and spinner dolphins more concentrated in the tropical waters off Mexico and along lat. 10°N, while striped and common dolphins tended to be found in the Central American Bight and along the Equator. This complementary type of distribution was less apparent with the more broadly distributed striped dolphin. It should be noted that our southern distributional lobe for spotted and spinner dolphins, at ca. lat. 5°S, may in part be due to the sampling pattern. However, the density of these dolphins along the Equator is definitely reduced, and we know of no information that does not suggest a rapid decline in density south of our lobe.

Our January-March data differs from the all-season data in indicating fewer schools in the area around the Revilla Gigedo Islands (at ca. lat. 19°N, long. 111°W) and between long. 90°W and 100°W along lat. 10°N for spotted and spinner dolphins. Also our data suggested that striped and common dolphins had a more localized distribution near the region of the Costa Rica Dome, and were relatively infrequent between long. 105°W and 120°W, along lat. 10°N. These differences may be due to seasonal changes in distribution.

The relative densities of these dolphins, as school encounter rates in the tuna purse seine fishery, were recently calculated by Polacheck (1983). The patterns he derived were fragmentary, but not inconsistent with those of this paper. He showed, for example, higher densities of spotted and spinner dolphins extending to the southwest from off southern Mexico and reduced densities in the Central American Bight. For striped and common dolphins, he also described a three-lobed distribution pattern as in this paper. However his equatorial lobe was centered just south of the Equator.

It seems likely that the dolphin community of the Upwelling-Modified Water differs from the Tropical Water community because of water-mass specific differences in the distribution and availability of food. This is supported by the different biotic features of Equatorial and Subtropical Waters relative to Tropical Waters. The distinction is clearly shown by the surface distribution of nutrients and primary production in these waters as measured during the EASTROPAC cruises (Love 1971, 1972). The equatorial waters of the eastern Pacific in particular are different. They support abundant plankton-feeding storm petrels rather than fish and cephalopod-feeding flocking birds that are usually abundant both north and south of the Equator (see also Love 1971, 1972 and King 1974). Dolphin species along the Equator tend not to be with fish or birds (Figs. 11, 12), and the species composition of the cetacean community appears to be distinct (Table 5; Au and Pitman 1981). Of course it has previously been known that equatorial waters are notable in being important sperm whale grounds (Townsend 1935) and have a zooplankton community distinct from other parts of the eastern tropical Pacific (McGowan 1972). Finally the fact that the common dolphin, a species characteristic of coastal upwelling waters from California to Peru, occurs with greater frequency in the equatorial waters and near upwelling areas in the Central American Bight, suggests that the shorter and different food chains of the upwelling environments (Parsons et al. 1977) may be the basis of the community difference.

The dolphin-tuna-bird association is one manifestation of community difference that is both striking and of ecological interest. The distribution of this association is notable in that it seems coincident with both the main habitats of spotted and spinner dolphins and the distribution of "surface" yellowfin tuna in the eastern Pacific (see Figure 11, Shingu et al. 1974, and Suzuki et al. 1978). Since it is primarily these dolphins that are associated with birds and with yellowfin tuna, the geography of the dolphin-bird association also defines that of the dolphin-yellowfin tuna association. This association of birds and fish with dolphins occurs in all tropical waters, including the southern Subtropical Water during the southern summer. It is apparently rare in equatorial waters of the eastern Pacific, in the central and western Pacific (Myazaki and Wada 1978; Au et al. fn. 2), and in the eastern tropical Atlantic (Levenez et al. 1980). In the central Pacific the same bird species found with spotted and spinner dolphins in the eastern tropical Pacific can be abundant (Gould 1974), and sooty terns especially, are frequently associated with small tunas, but these are most likely skipjack tuna (Murphy and Ikehara 1955; Waldrom 1964; Hida 1970; Blackburn and William 1975). Apparently those flocks seldom accompany dolphins or schools of larger yellowfin tuna. Yellowfin tuna and dolphins seldom seem to associate outside the eastern tropical Pacific.

The obvious feeding activity often seen in these joint aggregations of birds, spotted and spinner dolphins, and tuna suggests that these species have similar food and foraging requirements. Our observations indicate that the mammals and fish are not tightly associated in the aggregations (see Au and Perryman 1982) and probably feed independently (see also Norris and Dohl 1980a). However the tuna, birds, and spotted dolphin (at least) do appear to be feeding at the same time. Both the tuna and spotted dolphins feed on epipelagic fish and on squids (Perrin et al. 1973; Olson 1982), but the spinner dolphins feed differently and may forage more at night (Perrin et al. 1973; Norris and Dohl 1980b); though they are active in these feeding aggregations, they may not be directly associated with the tuna. Judging from the associations of bird and dolphin species, only spotted and spinner dolphins frequently find it advantageous to feed with yellowfin tuna. Furthermore the distribution of this association suggests that the necessary kind and behavior of prey that is likely the basis of the association appears characteristic of tropical, but not equatorial, waters. It occurs especially where a shallow thermocline may constrain the yellowfin tuna to the surface layer with the dolphins, a complex interaction between environment and physiology (Sharp 1978) that may cause the phenomenon known as "surface tuna". Finally the distribution of the bird-dolphin association indicates that the dolphin-tuna association is characteristic of areas of higher school density of spotted and spinner dolphins. High population densities of both dolphins and yellowfin tuna, and suitable prey are therefore likely requisites for joint dolphin-tuna schools. The dolphin-tuna association is a feature of the most productive tuna fishing zones of these tropical seas. In such rich areas, feeding tactics to exploit clumped prey could lead to multispecies aggregations of predators, as explained by Schoener (1982).

ACKNOWLEDGMENTS

This paper was reviewed by the following persons whose help is much appreciated: David E. Gaskin, Kenneth S. Norris, Carleton Ray, Gunter R. Seckel, Paul N. Sund, James G. Mead, Frank G. Alverson, Richard Pimentel, John A. McGowan, Gary T. Sakagawa, Jay Barlow, Andy Dizon, Albert C. Myrick, William Perrin, Steve Reilly, Tim Smith, Paul E. Smith, Rennie S. Holt, Eric D. Forsebergh, and Michael D. Scott.

We thank the officers and crews of the NOAA ships involved in this study, especially those of the *Townsend Cromwell* and *David Starr Jordan*, for their cooperation and help. We particularly thank the biological technicians who manned the watches through high-powered binoculars, for their keen observations and provoking discussions at sea. Among them we especially appreciate the work of Gary Friedrichsen, Phillip Unitt, James Lambert, Dale Powers, Robert Pitman, James Cotton, and Scott Sinclair.

We sincerely thank Lorraine Prescott and her staff for careful typing of this manuscript and Ken Raymond, Roy Allen, and Henry Orr for drafting the illustrations.

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ASPECTS OF THE LIFE HISTORY OF THE FLUFFY SCULPIN, *OLIGOCOTTUS SNYDERI*

MARY C. FREEMAN,[1] NATE NEALLY,[2] AND GARY D. GROSSMAN[1]

ABSTRACT

We examined age structure, growth rates, and diets of male and female *Oligocottus snyderi* Greeley at Dillon Beach, CA, where this sculpin numerically dominates the mid- and lower intertidal fish assemblage. Two age classes, 0+ and 1+, were present; maximum lifespan was about 1.5 years. Instantaneous population growth rates were highest for the 0+ age class, and most individuals attained spawning size during the first year of life. Growth rates for both age classes were highest during the high productivity Upwelling period and minimal during the low productivity, Oceanic-Davidson Current period.

Males and females primarily consumed gammarid amphipods and polychaetes. Larger individuals (≥50 mm SL) of both sexes consumed a wider variety of prey, including shrimps, crabs, and isopods. Among year and seasonal dietary changes were minimal. Females consumed two times more gammarids by weight than males during the low productivity Oceanic-Davidson Current period, when ovarian recrudescence occurs. Females may increase food consumption to meet the increased energetic demands of egg production.

Rapid sexual maturation and growth and the occurrence of recruitment during upwelling probably are adaptations to the pronounced annual cycle of productivity. These adaptations, together with intense utilization of an abundant prey (gammarids) not widely consumed by other assemblage members, probably contribute to *O. snyderi*'s numerical dominance in the rocky intertidal of central California.

The fluffy sculpin, *Oligocottus snyderi* Greeley, is a common species which inhabits the rocky intertidal from Baja California to Sitka, AK (Miller and Lea 1972). Between central California and British Columbia, *O. snyderi* frequently is very abundant (Green 1971; Cross 1981; Yoshiyama 1981; Grossman 1982). This species occurs primarily in mid- and lower intertidal areas (Green 1971; Yoshiyama 1981), and often is associated with surfgrass (Green 1971; Nakamura 1976a). The general absence of this species from the high intertidal is probably due to its inability to tolerate higher temperatures which frequently occur in high intertidal pools (Nakamura 1976b).

Life histories of intertidal fishes, particularly cottids, are poorly known (Gibson 1969, 1982). Published information on the demography of *O. snyderi* is restricted to the work of Moring (1981), who examined age structure of a northern California *O. snyderi* population, and Grossman and deVlaming (1984), who described the species' reproductive ecology. This paper presents data on age structure, growth rates, and dietary habits of an *O. snyderi* population at Dillon Beach, CA, a site that is subject to pronounced annual cycles of oceanic productivity (Parrish et al. 1981). *Oligocottus snyderi* numerically dominates the intertidal fish assemblage at Dillon Beach (Grossman 1982); the present study explores demographic and ecological characteristics which may account for this species' ecological success in the rocky intertidal.

MATERIALS AND METHODS

Collections

Oligocottus snyderi were collected from a series of mid- and lower intertidal pools at Dillon Beach, CA, on 15 dates from January 1979 to July 1981 (see Grossman in press a for sampling dates). Repeated collecting did not affect assemblage structure (Grossman 1982, in press a). Fish were obtained by spreading a 10% solution of quinaldine in isopropanol through the pools and then collecting individuals after anesthetization. Over 1,400 *O. snyderi* were collected. Specimens were preserved in buffered Formalin[3] and were later washed and transferred to 45% isopropanol. Individuals were measured to the nearest millimeter standard length (SL) and weighed to the nearest 0.1 g. Sexes of all

[1]School of Forest Resources, University of Georgia, Athens, GA 30602.

[2]Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

individuals collected during 1979 and of specimens used for gut analysis also were recorded. A complete description of collecting methods and the study site are presented in Grossman (1982, in press b).

Collection dates were assigned either to the Upwelling or the combined Oceanic-Davidson Current (ODC) oceanographic seasons, based on water temperature and a calculated upwelling index (see Grossman in press b). The Upwelling period is characterized by frequent upwelling of nutrient-rich waters and high productivity (Bolin and Abbott 1963; Garrison 1979). In contrast, the ODC period exhibits minimal upwelling, frequent downwelling, and low productivity (Bolin and Abbott 1963; Garrison 1979). Data from individuals collected during the latter seasons were pooled because these periods were not readily distinguishable (Grossman in press b). Consequently, comparisons of *O. snyderi* food habits and length-weight relationships represent contrasts between a high productivity period (Upwelling, all months from April to August, plus March 1980) and the low productivity ODC period (October-February, plus March 1979). Monthly mean water temperatures ranged from 9.7° to 11.9°C during the Upwelling period from 11.2° to 14.2°C during the ODC period (Grossman in press b).

Length-Weight and Growth Calculations

Regressions of individual weight versus standard length were calculated separately for males and females collected in the Upwelling and ODC periods. Regression equations were of the form $W = aL^b$, fitted as $\ln W = \ln a + b \ln L$. Slopes (b) of regression equations for males and females were compared for each period by analysis of covariance (ANCOVA). Seasonal differences between slopes also were examined for each sex.

Regression slopes for the two sexes and periods were divided by their correlation coefficients to estimate slopes for geometric mean functional regressions of weight versus length (Ricker 1973). Functional regressions are recommended for describing relations between weight and length because both variables are subject to natural variability (Ricker 1973). Functional regression slopes were used to derive y-intercepts from the equation $y\text{-int.} = \bar{y} - (b/r)\bar{x}$ (Ricker 1973). These slope estimates were employed to calculate instantaneous rates of growth in weight (G) as

$$G = (b/r)(\ln L_2 - \ln L_1), \text{ (Ricker 1975),}$$

where b/r = slope of the functional length-weight regression;
L_1 = mean length at the time t; and
L_2 = mean length at time $t + 1$.

Growth rates were calculated for individual year classes which were separated using length-frequency distributions. To compare growth rates for males and females, t-tests for paired samples were used.

Sex ratios for the 1979 samples were tested for deviations from unity using chi-square tests corrected for continuity.

Dietary Analyses

Stomach contents were removed from a subsample (597 total) of the *O. snyderi* collected between January 1979 and July 1981. Ninety-seven percent of stomachs examined contained food. Prey were identified to the lowest possible taxon and weighed (wet) to the nearest milligram. The weights of each prey type were pooled separately for males and females from each collection. Diets were then calculated as the percent of the total stomach content weight attributable to each prey type. The number of fish containing each prey type (i.e., prey frequency of occurrence, henceforth FO) also was recorded.

Dietary data were pooled across collections within the Upwelling and ODC periods for each sex, to compare feeding habits between sexes and seasons. Because the study period spanned 3 yr, it also was possible to quantify among year variability in seasonal and sex-specific feeding habits. Sex-linked ontogenetic dietary changes were examined by separating males and females into 20 mm size classes and comparing prey consumed by each size class in different seasons and years. Niche breadth was calculated as $\Sigma\ 1/p_i^2$ (Levins 1968), where p_i is the proportion of the total prey weight comprised of the ith prey type. Only prey types constituting at least 1% of the total prey weight were included in niche breadth calculations. Niche breadth was compared among size classes by using the Wilcoxon signed-rank test.

RESULTS

Length-Weight Relationships

The slope for the male length-weight regression for the Upwelling period was significantly greater than that for females (ANCOVA, $F = 12.875$, $P < 0.001$; Table 1). Slopes of length-weight regressions for males and females collected during the ODC period were not significantly different (ANCOVA,

TABLE 1.—Length-weight relationships, described as $W = aL^b$, for *Oligocottus snyderi*. Coefficients for the least-squares (ln W = ln a + b ln L) and functional (ln W = ln a' + (b/r) ln L) regressions are presented, as well as the correlation coefficients for the least-squares regressions (r) and the number of individuals used in each regression (N). ODC = Oceanic-Davidson Current.

			Least-squares regression		Functional regression	
	N	r	a	b	a'	b/r
Males						
Upwelling	150	0.984	0.0000178	3.097	0.0000146	3.147
ODC	112	0.973	0.0000253	2.991	0.0000182	3.075
Females						
Upwelling	164	0.972	0.0000472	2.835	0.0000346	2.917
ODC	131	0.976	0.0000202	3.069	0.0000151	3.143

$F = 0.736$, $P > 0.25$). Seasonal comparisons for each sex showed that the male Upwelling and ODC slopes were not significantly different (ANCOVA, $F = 1.483$, $P > 0.10$), whereas the females had a significantly higher slope during the ODC period (ANCOVA, $F = 6.147$, $P < 0.025$).

Growth Rates

Length-frequency histograms for *O. snyderi* at Dillon Beach indicated that two year classes were present on most dates (Fig. 1). Recruitment began in spring and peaked during summer. The onset of recruitment differed between years. Age 0+ fish were first taken in May of 1979; however, in 1980 recruitment began in March. Age 0+ individuals of the 1979 cohort grew 20 mm in length (from 20-25 to 40-55 mm SL) by December of their first year. Members of the 1978 cohort (= age 1+ fish) increased in length from 40-55 to 60-70 mm SL during spring, summer, and fall 1979. Individuals did not appear to survive a second winter during 1980, although a few males recruited in 1977 may have survived until spring of 1979 (Fig. 1).

Sex ratios for the 0+ age class were significantly different from unity in the August 1979 collection in which there were significantly more males than females (1.7:1; $\chi^2 = 7.32$, $P < 0.01$). Age 1+ females significantly outnumbered males in January 1979 (4:1; $\chi^2 = 6.05$, $P < 0.025$), July 1979 (1.8:1; $\chi^2 = 4.38$, $P < 0.05$), and December 1979 (3:1; $\chi^2 = 5.04$, $P < 0.025$).

Instantaneous growth rates were calculated for males and females from the two year classes present in 1979 (Table 2). Prolonged recruitment (lasting from May through August) resulted in apparent depressed spring and summer growth rates for the age 0+ class when all individuals were included in the calculations of mean lengths (Table 2). Therefore, fish which appeared to have been recruited later than the majority of the class were excluded from consideration in the June, July, and August calculations, as shown in Figure 1. Only the very large males collected in January 1979 were excluded from the age 1+ mean length calculations, as these individuals apparently were survivors from the 1977 year class and probably died shortly thereafter. The highest monthly instantaneous growth rates were obtained during May and June, averaging 0.860 and 0.655 for age 0+ males and females, and 0.209 and 0.188 for age 1+ males and females (Table 2, Fig. 2). Growth rates markedly decreased after August, averaging 0.065 and 0.169 for age 0+ males and females, and 0 and 0.061 for age 1+ males and females during October and November (Table 2, Fig. 2).

Males and females attained nearly equal lengths in the first season of growth; however, age 1+ males displayed significantly greater mean lengths (t-tests, $P << 0.05$) than age 1+ females from June through November 1979 (Fig. 2). Growth rates were not significantly higher for males than females in either size class when compared from January to December 1979 (age 0+: $t = 1.002$, $P > 0.1$; age 1+: $t = 1.232$, $P > 0.1$); however, if only the data from January to October are included for the age 1+ class, males did have significantly higher growth rates ($t = 2.255$, $P < 0.05$). This discrepancy is caused by the low numbers of age 1+ fish collected in November (14) and December (24). Length-frequency histograms (Fig. 1) also show that age 1+ males are larger than females, whereas length distributions are

TABLE 2.—Instantaneous growth rates of *Oligocottus snyderi* males and females in their first (age 0+) and second (age 1+) years of growth. Rates were calculated for the intervals between the 1979 collections. Values in parentheses were calculated with all individuals included in the age 0+ cohort (see text).

Collection dates	Instantaneous growth rate			
	Age 0+		Age 1+	
	Males	Females	Males	Females
1-27-79				
	—	—	0.257	0.079
3-26-79				
	—	—	0.295	0.171
5-16-79				
	1.059 (1.059)	0.718 (0.562)	0.318	0.204
6-13-79				
	0.661 (0.429)	0.591 (0.358)	0.099	0.171
7-12-79				
	0.352 (0.306)	0.295 (0.390)	0.111	0.074
8-09-79				
	0.303 (0.582)	0.124 (0.419)	0.164	0.063
10-07-79				
	0.129	0.149	0	0.122
11-04-79				
	—	0.188	—	—
12-04-79				

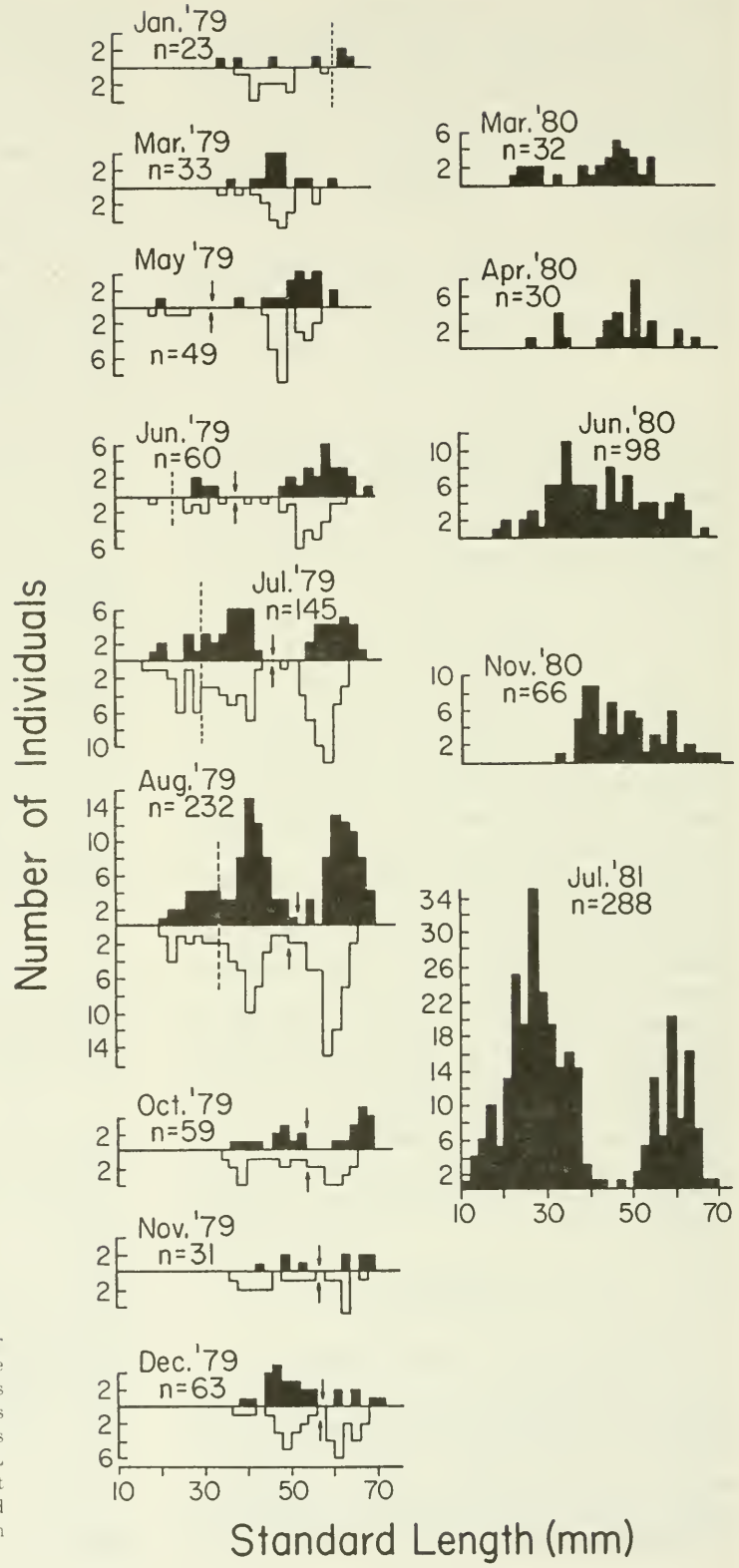

FIGURE 1.—Length-frequency distributions for *Oligocottus snyderi*. Males and females are separated in the 1979 collections, with females shown below the axis. Arrows indicate divisions between year classes 0+ and 1+, and broken lines designate limits for inclusion in cohort mean SL calculations (January, June, July, and August 1979). The 1980 and 1981 collections are included for comparison, but the sexes are not shown separately.

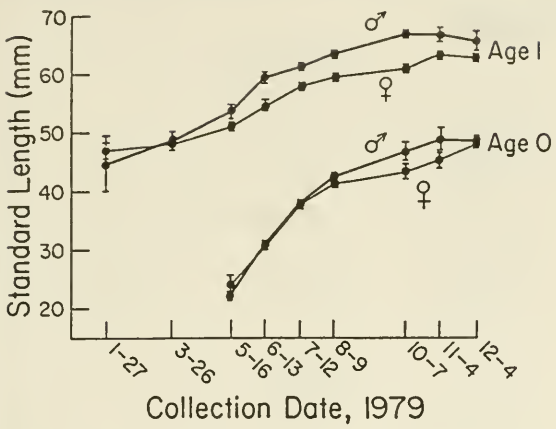

FIGURE 2.—Growth curves for age 0+ and 1+ *Oligocottus snyderi*. The standard lengths ($\bar{x} \pm$ SE) of each sex in the two age classes are shown for the 1979 collections. June, July, and August age 0+ SLs do not include late recruited individuals (see text and Figure 1).

about equal for age 0+ males and females. The low mean lengths calculated for age 0+ females in October and November resulted from the inclusion of small individuals probably recruited late in Upwelling, but which were not easily separable from the remainder of the cohort. Hence, calculated growth rates probably underestimate age 0+ female growth from August to October and overestimate growth from October to December.

Dietary Habits

Oligocottus synderi's diet at Dillon Beach consisted primarily of gammarid amphipods and polychaetes. Summed across all collections, gammarids composed 78% and 66% of the gut contents of females and males, respectively. Polychaetes totaled 10% of the female diet and 14% of the male diet. Shrimp remains, mainly *Heptacarpus taylori*, contributed 5% and 4% to female and male diets, respectively. A total of 20 prey taxa were consumed by *O. snyderi*; however, no other prey category composed more than 3% of the diet, with the exception of unidentifiable hard-bodied prey remains, which totaled 5% of the gut contents of males. Dietary breadth based on all collections was higher for males than females (2.17 vs. 1.61), because males consumed greater amounts of minor prey types.

The major seasonal dietary changes for both males and females were decreased gammarid consumption and increased polychaete consumption during Upwelling as compared with the ODC period (Tables 3, 4). Dietary breadth also was greater for both sexes during Upwelling than in the ODC period (2.02 vs. 1.44 for females, and 2.19 vs. 2.09 for males). Differences were observed between male and female diets. Specifically, in the ODC period, gammarids composed a greater proportion of female than male diets (83% vs. 68%), whereas males consumed proportionately more eggs, *Idotea* spp. (Isopoda), and crabs (Table 4). Although standard lengths and weights of ODC males (138) and females (132) used for gut analyses were not significantly different (SL: $t = 1.058$, $P > 0.1$; weight: $t = 1.036$, $P > 0.1$), females had significantly greater amounts of food in their stomachs ($t = 4.857$, $P = 0.0001$, Table 4). This difference is attributable to the weight of ingested gammarids because 131 (FO) females contained a total of 8.4 g of gammarids, whereas 132 males contained only 4.3 g (total weight).

Examination of food habits across size classes shows that larger individuals generally possessed a more diverse diet than smaller individuals (Figs. 3, 4). Dietary breadth was significantly higher (Wilcoxon signed-rank test, $n = 12$, $T = 69$, $P < 0.01$) for 50-69 mm SL fish than for 30-49 mm SL individuals when compared across both sexes for all years. Individuals <30 mm SL consumed mainly gammarids and isopods; polychaetes and shrimp were major prey only for larger fish. *Pagurus* spp. and crabs, including *Cancer* spp. and *Pachycheles* spp., were found only in individuals ≥40 mm SL.

The general observation of decreased gammarid consumption by larger *O. snyderi*, concomitant with increased polychaete and shrimp consumption, applies to collections made throughout the 3-yr study period. The majority of among year variation in food habits resulted from the presence of large, rare prey items in single individuals (Figs. 3, 4). An exception was the high consumption of polychaetes by males collected in July 1981 (Fig. 3). In this case, polychaetes occurred in all of the 50-69 mm fish and in 56% of the 30-49 mm fish, and composed a considerably higher proportion of the diet than during previous Upwelling collections.

DISCUSSION

Age-Structure and Growth

At Dillon Beach, a habitat displaying marked seasonal fluctuations in productivity (Grossman 1982, in press b; Grossman and deVlaming 1984), *O. snyderi* is short lived, with a maximum lifespan of about 1.5 yr and a maximum length of about 70 mm SL. Whereas two age classes were observed in this study, Moring (1981) observed as many as three age classes in Trinidad Bay. Standard lengths attained

TABLE 3.—Food habits of male and female *Oligocottus snyderi* collected during the Upwelling period. Values shown for each prey type are total weight ingested, percent of total prey weight, and frequency of occurrence (FO).

$\bar{x}$ SL ± SD	Females, n = 164 45.9 ± 11.7 mm			Males, n = 150 51.3 ± 11.8 mm		
Prey	Wt. (g)	% Wt.	(FO)	Wt. (g)	% Wt.	(FO)
Gammarids	3.850	68	(125)	3.653	64	(132)
Polychaetes	0.980	17	(19)	1.109	19	(33)
Heptacarpus taylori	0.202	4	(4)	0.222	4	(5)
Crangon	0.146	3	(2)	0		
Other shrimp	0.001	<1	(1)	0.004	<1	(1)
Hard-bodied prey rem.	0.196	3	(18)	0.494	9	(20)
Isopods	0.095	2	(10)	0.074	1	(19)
Idotea	0.006	<1	(2)	0.049	1	(3)
Pagurus	0.067	1	(1)	0		
Crabs	0.036	1	(2)	0.026	<1	(1)
Algae	0			0.039	1	(9)
Snails	0.024	<1	(4)	0.010	<1	(3)
Caprellids	0.026	<1	(1)	0.004	<1	(2)
Soft-bodied prey rem.	0			0.014	<1	(1)
Barnacle cirri	0			0.012	<1	(5)
Total	5.629	99		5.710	99	

TABLE 4.—*Oligocottus snyderi* feeding habits during the combined Oceanic-Davidson Current periods. Values shown for each prey are the weight ingested, percent of total prey weight, and frequency of occurrence (FO).

$\bar{x}$ SL ± SD	Females, n = 132 49.5 ± 8.8 mm			Males, n = 138 50.6 ± 9.3 mm		
Prey	Wt. (g)	% Wt.	(FO)	Wt. (g)	% Wt.	(FO)
Gammarids	8.418	83	(131)	4.278	68	(132)
Polychaetes	0.611	6	(20)	0.587	9	(23)
Heptacarpus taylori	0.304	3	(3)	0.308	5	(4)
Crangon	0.089	1	(2)	0		
Other shrimp	0.071	1	(1)	0		
Eggs	0.008	<1	(1)	0.397	6	(6)
Idotea	0.131	1	(6)	0.252	4	(14)
Isopods	0.255	3	(19)	0.104	2	(16)
Sea anemones	0.147	1	(2)	0		
Hard-bodied prey rem.	0.053	1	(2)	0.086	1	(4)
Pachycheles	0			0.091	2	(1)
Barnacle cirri	0.001	<1	(1)	0.075	1	(5)
Pagurus	0.043	<1	(2)	0		
Bivalves	0			0.036	1	(1)
Algae	0			0.044	1	(9)
Caprellids	0.015	<1	(2)	0.003	<1	(1)
Cancer	0			0.005	<1	(1)
Crabs	0			0.002	<1	(1)
Snails	0.002	<1	(1)	0		
Total	10.148	100		6.268	100	

by the 0+ and 1+ age classes observed by Moring (1981) were similar to those displayed by the Dillon Beach age 0+ and 1+ classes; however, Moring observed age 2+ individuals of up to 101 mm SL. Nakamura (1976a, b) also reported collecting *O. snyderi* >80 mm SL at Port Renfrew, British Columbia. These results indicate that *O. snyderi* may have a longer lifespan at more northerly locations. The scarcity of individuals >70 mm SL at Dillon Beach probably did not result from repeated sampling because such large individuals were absent from the initial samples and from collections made in previously unsampled pools near the study site in August 1979, December 1979, and April 1980. There was no discernable pattern in sex-ratio deviations from unity observed in four 1979 collections, which

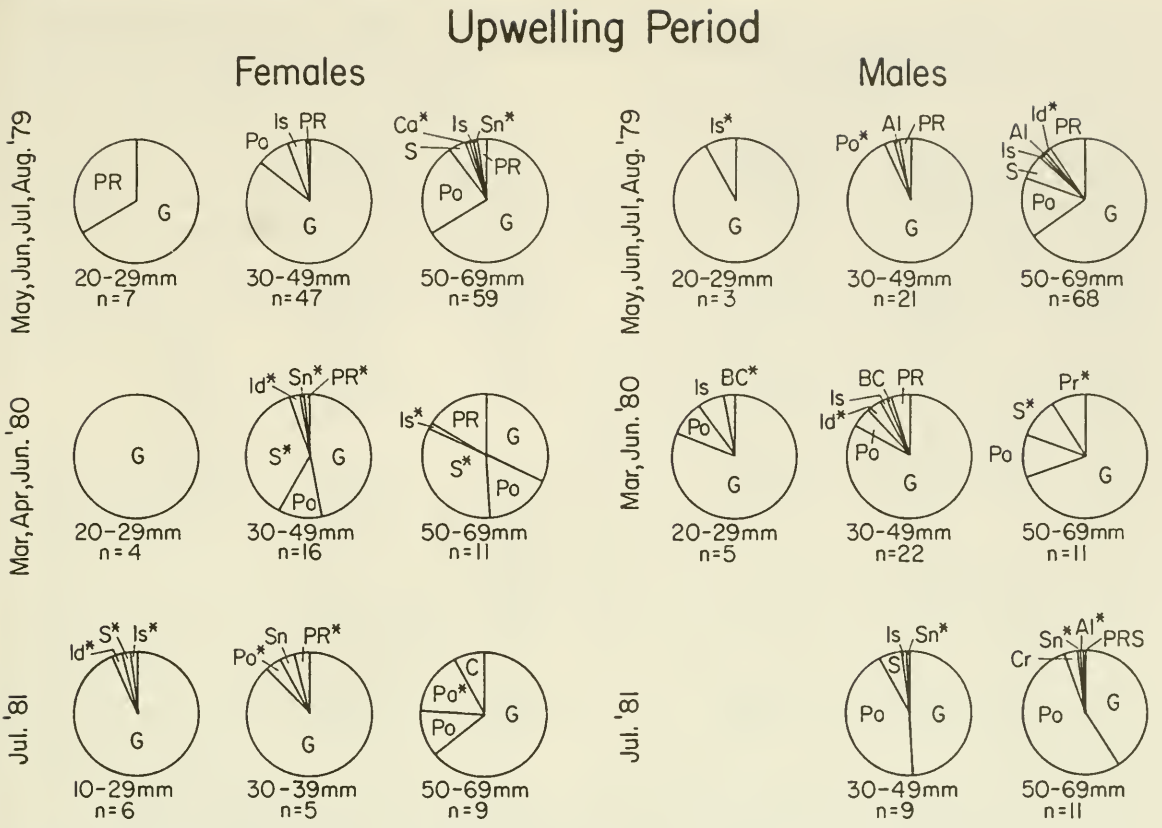

FIGURE 3.—Sex-specific ontogenetic and among year variation in *Oligocottus snyderi* feeding habits during the 1979, 1980, and 1981 Upwelling periods. Prey are represented as percent total prey weight, and only prey composing ≥1% of the total prey weight are shown. Asterisks indicate prey which occurred in only one individual. Prey abbreviations are G (gammarids); PR (hard-bodied prey remains); Po (polychaetes); Is (isopods); S (shrimps, all spp.); Ca (caprellids); Sn (snails); Id (*Idotea* spp.); Pa (*Pagurus* spp.); Cr (crabs, all spp.); Al (algae); and BC (barnacle cirri).

suggests that males and females have about equal lifespans at Dillon Beach.

Oligocottus maculosus Girard, another abundant intertidal cottid (Nakamura 1976a, b; Moring 1981), was estimated by Chadwick (1976) to survive as many as five growing seasons, based on counts of vertebral rings, at Port Renfrew, B.C., and Bruels Point, CA. Annuli were not validated in this study, however, and it is questionable if the rings observed were actually formed once yearly. In addition, Chadwick's (1976) growth rate estimates are extremely low, suggesting that *O. maculosus* grew no more than 7 mm in any season after the first. Moreover, all previous studies of both *O. snyderi* (Moring 1981) and *O. maculosus* (Atkinson 1939; Green 1971; Moring 1979) showed that populations of these species were composed primarily of age 0+ and 1+ individuals, as was *O. snyderi* at Dillon Beach. Consequently, it appears unlikely that *O. maculosus* survives to age 5+ as suggested by Chadwick (1976), and in any case such longevity was not observed for *O. snyderi* at Dillon Beach.

Intertidal fishes appear to display several distinct life history patterns. Short lifespan (1-3 yr), early maturation, and high reproductive effort have been reported for several intertidal gobies in northern temperate habitats (Gibson 1969, 1982; Grossman 1979; Miller 1979). In contrast, lifespans of 4 to over 10 yr, accompanied by delayed maturation, have been observed in many intertidal species, including gobiids and blenniids (Gibson 1969, 1982; Stephens et al. 1970; Grossman 1979; Miller 1979). Little information is available for intertidal cottids. The largest North American cottid, *Scorpaenichthys marmoratus* Ayers, may live 13 yr, but only inhabits tidepools during its first or second year of life (O'Connell 1953; Grossman and Freeman unpubl. data). Another large sculpin, *Leptocottus armatus* Girard, common in the Pacific coast bays and estuaries, is known to live to age 3 and reaches sexual maturity

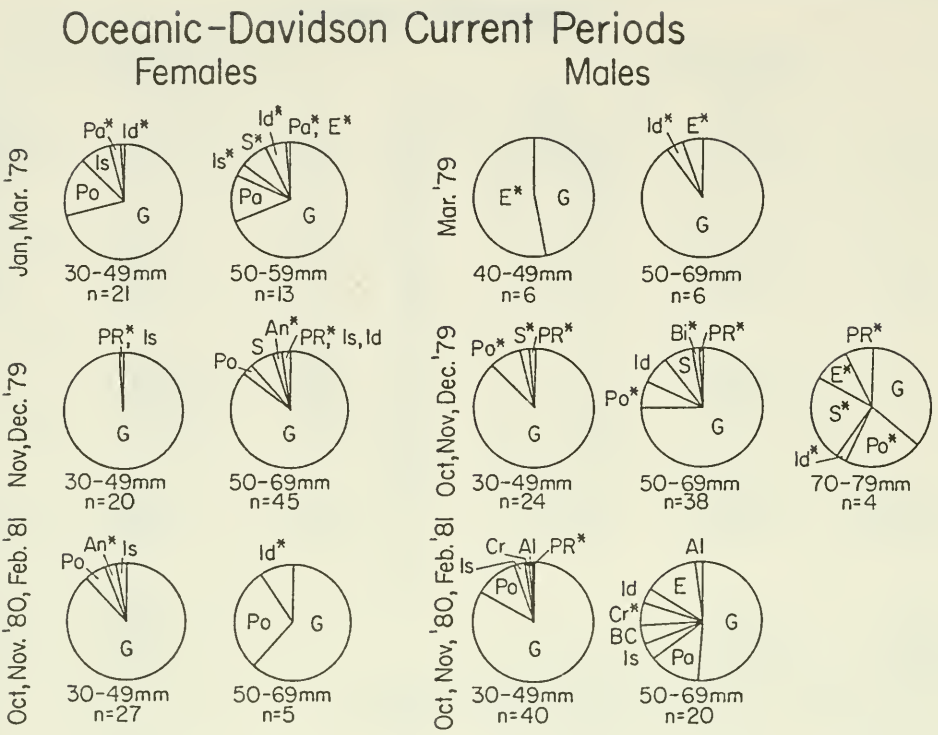

FIGURE 4.—Sex-specific ontogenetic and among year variation in *Oligocottus snyderi* feeding habits during the three ODC (Oceanic-Davidson Current) periods encompassed by this study. Prey are represented as percent total prey weight; only prey composing ≥1% total prey weight are shown. Asterisks indicate prey occurring in only one individual. Abbreviations are as in Figure 3, with the addition of E (eggs); An (sea anemones); and Bi (bivalves).

after 1 yr (Jones 1962; Tasto 1975). *Oligocottus snyderi* and *O. maculosus* apparently are best characterized by the short lifespan, early maturation, life history pattern. This conclusion is based on growth rate data coupled with the scarcity of individuals older than 1.5 yr, and data showing early maturation and high reproductive effort for *O. snyderi* (deVlaming et al. 1982).

The majority of age 0+ *O. snyderi* at Dillon Beach attained sufficient size to spawn during their first year; it is less certain what proportion of these individuals survive to spawn in their second year. Grossman and deVlaming (1984) indicated that, at Dillon Beach, females mature at about 40 mm SL and contain vitellogenic oocytes from October through May. These females also probably spawn more than once, primarily during winter and spring (Grossman and deVlaming 1984). Length-frequency distributions from March and May 1979 and March and April 1980 show that a single age class dominated the population. Hence, assuming that recruitment primarily was derived from this population, age 1+ individuals (recruited the previous spring and summer) must have been responsible for nearly all spring spawning. The paucity of large individuals (i.e., >60 mm SL) in winter or spring samples indicates that if individuals spawned in their second year, this reproduction must have occurred prior to January. Substantial numbers of age 1+ individuals were captured from October to December 1979 and in November 1980. Although the earliest recruitment observed at Dillon Beach occurred in March 1980, Moring (1981) captured newly recruited individuals as early as January. This suggests that fall spawning may occur in more northerly populations of *O. snyderi*.

Reproduction apparently is timed to insure that larvae metamorphose during upwelling. Grossman (1982) found a significant correlation between upwelling activity and the number of resident species with young-of-the-year present at Dillon Beach. Grossman and deVlaming (1984) also observed that *O. snyderi* recruitment was strongly correlated with productivity; the authors pointed out that the early

recruitment observed in March 1980 coincided with the onset of upwelling, whereas both recruitment and upwelling were delayed until May 1979.

If some individuals do survive to reproduce during their second year, the larger sizes attained by males during their second growing season may be advantageous during spawning. This is because male *O. snyderi* have a lengthened and prehensile first anal ray with which they clasp females during copulation, and the larger a male is in relation to a female, the more efficiently he will be able to clasp her (Morris 1956).

Dietary Habits

Oligocottus snyderi at Dillon Beach consumed primarily gammarid amphipods and polychaetes. These data are consistent with previous observations (Johnston 1954; Nakamura 1971; Yoshiyama 1980), although they differ somewhat from results obtained by Cross (1981) from two sites in northern Washington. Cross (1981) reported that harpacticoid copepods were a major prey for *O. snyderi* at one site; similarly, polychaetes also were consumed only at one site. However, Cross (1981) also observed high gammarid consumption by *O. snyderi*, as well as by most other intertidal species he studied. In addition, gammarids have been cited as a major prey in other intertidal fish assemblages (Mitchell 1953; Johnston 1954; Zander 1979, 1982; Grossman in press b). At Dillon Beach, gammarids frequently were consumed by resident and seasonal intertidal fishes, although only one other resident (*Apodichthys flavidus* Girard) possessed a diet dominated by gammarids (Grossman in press b). Among year, seasonal comparisons, however, show that a variety of minor prey types also are consumed by *O. snyderi*.

Combinations of shrimps, crabs, hermit crabs, *Idotea*, and other irregularly consumed prey constituted a considerable proportion of *O. snyderi*'s diet throughout the year. This was particularly evident in larger fish, which suggests that capture of these prey is either more difficult for small fish due to morphological, physiological, or behavioral constraints, or involves increased predation risk. Similarly, a shift from gammarids to larger prey concomitant with increasing length was observed for the majority of intertidal fishes at Dillon Beach (Grossman in press b), and for some species studied by Cross (1981). In contrast, Yoshiyama (1980) was unable to detect dietary differences between small and large *O. snyderi*, or two other intertidal cottids. Yoshiyama pooled small samples collected throughout a year, however, which may have obscured seasonal changes in prey consumption. Because his samples were small, Yoshiyama also may have underestimated consumption of rare prey.

Although seasonal dietary changes were minor, there is evidence that females possessed higher ingestion rates than males during the ODC period. During this season of lowered productivity, females consumed two times more gammarids (by weight) than males, although mean fish length and gammarid frequency of occurrence were nearly identical between sexes. This difference between consumption rates may not be artifactual. Females develop and carry vitellogenic eggs during this period (Grossman and deVlaming 1984), and consequently have high energy demands. There was no evidence that intersexual or ontogenetic dietary differences resulted from differential distribution or collection disturbance.

The high prey weight observed in males and females collected during the ODC period is of interest in light of the low growth rates observed during winter months. Moring (1979, 1981) also observed cessation of growth during winter for both *O. snyderi* and *O. maculosus* in northern California. He suggested that reduced foraging activity caused by increased wave action during winter might partially explain this growth reduction. Dietary data from Dillon Beach do not support this conclusion because ODC specimens contained a greater total weight of prey than individuals collected during Upwelling, even though a greater number of individuals were examined during the latter period. The Dillon Beach study site probably is more sheltered from winter storm activity, however, than the Trinidad Bay sites observed by Moring (Grossman pers. obs.). In the absence of ingestion rate data for both seaons, results based on gut content weight alone are equivocal. Moring (1981) also suggested that gonadal development during the winter months might be responsible for reduced growth; this could also apply to *O. snyderi* at Dillon Beach.

In conclusion, *O. snyderi* the most abundant intertidal cottid at Dillon Beach, possesses a suite of characteristics which suggest that productivity has influenced the biology and behavior of this species. For example, *O. snyderi* reaches sexual maturity during its first year of life, and spawns at a time which enables recruitment to take place during the season of highest productivity (i.e., Upwelling (Grossman and deVlaming 1984)). Grossman (1982, in press b) presented strong evidence that productivity cycles also affect many other species at Dillon Beach, because this assemblage appears to be organized through interspecific exploitative competition for

food. Recuitment and numerical abundances within this assemblage also were strongly correlated with productivity (Grossman 1982). *Oligocottus snyderi* possesses a variety of adaptations (e.g., rapid maturation, high female reproductive effort, utilization of an abundant prey not widely consumed by other assemblage members) which probably are responsible for its numerical dominance in a fluctuating environment.

ACKNOWLEDGMENTS

We thank the many friends and colleagues who aided in the collection and analysis of data. Jeff Barrett, Dan Erickson, Doug Facey, Margi Flood, Steve Floyd, and Joe Hightower reviewed the manuscript and their comments are greatly appreciated. We also appreciate the help of Bonnie Fancher who typed various drafts of this manuscript.

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VARIABILITY, TRENDS, AND BIASES IN REPRODUCTIVE RATES OF SPOTTED DOLPHINS, *STENELLA ATTENUATA*

JAY BARLOW[1]

ABSTRACT

Temporal changes were examined in three parameters that affect reproduction of spotted dolphin populations in the eastern Pacific. Of mature females, percent pregnant decreased markedly from the period 1971-73 to the period 1974-83. Within the period 1974-83, percent pregnant remained relatively constant. Of pregnant females, percent lactating increased during the period 1971-83. The percentage of sexually mature females did not change. Potential biases in the measurement of the three parameters were identified by examining the effects of sampling conditions. The percentage of mature females that are pregnant and the percentage of pregnant females that are lactating were found to be robust to sampling conditions. The percentage of mature females in a sample was found to depend significantly on the number of dolphins killed per set, and annual variability was too large to be explained by random sampling error. Comparisons between two populations show that the more exploited population has a lower percent pregnant, although the opposite might be expected from density compensatory effects. Percent lactating and percent immature were higher in the more exploited population.

Changes in the reproductive parameters of cetacean populations can be used to make inferences about the status or general "health" of a population. For instance, increases in pregnancy rates and decreases in the age at attainment of sexual maturity were linked to reductions in Antarctic whale populations (Gambell 1975). Re-analysis of these data, however, revealed unsuspected biases, and Gambell's results are now being questioned (Mizroch 1983). The purpose of this paper is to examine potential biases in measuring reproductive rates of spotted dolphins, *Stenella attenuata*. This species is taken incidentally in the tuna purse seine fishery in the eastern tropical Pacific (Smith 1983). The intent is to determine whether reproductive rates can be measured with sufficient precision to monitor intrapopulation changes or to make interpopulation comparisons.

Previous studies of female reproduction in spotted dolphins of the eastern Pacific have shown an apparent decrease in pregnancy rates from 1973 to 1975 (Perrin et al. 1977), from 1973 to 1978,[2] and from 1971 to 1978 (Hester 1984). Hester (1984) suggested that this decline in pregnancy rates is related to the decline in fishing-related dolphin mortality during the same time period.

Three indices of the reproductive status of female spotted dolphins are examined in the present paper: 1) the fraction of sexually mature individuals that are pregnant, 2) the fraction of pregnant females that are lactating, and 3) the fraction of females that are sexually mature. These measures have been used previously in calculating what has been termed the gross annual reproductive rate (GARR) of spotted dolphins (Perrin et al. 1976). This paper reexamines data from 1971 to 1978 plus additional data from 1979 to 1983 to determine whether the previously noted trends in reproductive rates are real, and if so, whether they are continuing. Also, factors are examined which may be biasing estimates of reproductive rates and which could be causing spurious changes in apparent pregnancy rates and GARR. Finally, differences in these reproductive indices between two geographic stocks of spotted dolphin are discussed in view of their different histories of incidental fishing mortality.

MATERIALS

Reproductive data were collected from a sample of the dolphins killed in tuna purse-seining operations in the eastern tropical Pacific (ETP). Three stocks of spotted dolphins are recognized in this area based on morphological differences (Perrin et al. 1979). Samples considered here include two of these: the northern offshore stock which has been subject to tuna fishing since 1959 and the southern offshore stock which has been subject to exploitation since

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2]Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rate of gross annual reproduction in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-78. Admin. Rep. LJ-80-02, 51 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Manuscript accepted January 1985.
FISHERY BULLETIN: VOL. 83, NO. 4, 1985.

the early 1970's. In 1971 and 1972, field technicians collected samples predominantly from females with the "adult" or fused color pattern (Perrin 1970). Beginning in 1973, field technicians were instructed to collect samples nonselectively with respect to size and sex. Operationally, this meant working-up specimens in the order in which they appeared on the deck of the tuna vessel. Sampling methods and laboratory procedures are described in detail by Perrin et al. (1976). Sample locations are shown in Figure 1.

Reproductive tracts of mature and nearly mature females were preserved in the field for laboratory examination. In 1971 and 1972, the definition of "mature and nearly mature" was not explicit. In 1973, "mature and nearly mature" was defined as individuals with "mottled" or "fused" developmental color phases (Perrin 1970). Because females in the younger "speckled" color phase occasionally were found to be pregnant, "mature and nearly mature" was redefined operationally (beginning in 1974) as specimens >150 cm total length (TL, measured from tip of rostrum to fluke notch). Laboratory examination of preserved ovaries was used to determine the presence of corpora from past ovulations. Pregnancy was determined by visual examination of the uterus (in later years, fetuses >30 cm TL were removed and measured in the field). Mammary glands were slit and checked in the field for the presence of milk.

In addition to the above life history information, field technicians collected data pertaining to conditions under which the samples were taken. Information used in this report includes the observer's estimate of the size of the school from which the sample was taken, the duration of the chase before the net was set, the number of dolphins known to be killed during fishing operations, and the geographic location at which the sample was taken.

METHODS

Three indices of female reproduction are considered in this paper: the percent pregnant, the percent lactating, and the percent mature. Temporal trends in these three indices were examined by regressing annual means against year (weighting by the inverse of binomial variances).

In calculating the percentages of mature females that were pregnant and that were lactating, specimens were used only if both ovaries were collected and if at least one corpus of ovulation (corpus albicans or corpus luteum) was present. Previously, 1971 and 1972 samples were excluded from calculation of percent pregnant because of undersampling of younger females with a mottled color pattern (Perrin et al. 1977). This was not deemed necessary in this study, because in 1973-83 samples the percent pregnant for mature mottled females (31.1%) was essentially the same as that for mature females with a fused color pattern (31.4%).

In calculating the percentage of females that were sexually mature, two different criteria were used for determining maturity. In the majority of cases both ovaries were examined, and the presence of one (or more) corpus of ovulation was taken as evidence of sexual maturity. If ovaries were not collected or examined (which was true for about 30% of females over 150 cm TL), a length criterion was used for maturity. Samples from 1971 and 1972 were excluded from these analyses because sampling was not random in those years.

"Length at attainment of sexual maturity" was determined by the method used by Perrin et al. (1977). Based on the sample for which ovaries were examined, this length was estimated as the length at which the number of longer immature individuals equals the number of shorter mature individuals. For the northern stock, the length at the onset of sexual maturity was determined independently for each year 1974-83 (176.5, 177.5, 177.0, 177.0, 178.0, 177.5, 179.0, 178.5, 180.0, and 182.0 cm, respectively). In 1973 the decision to collect ovaries was not based on specimen length. The apparent trend in these data yields a significant regression (P = 0.0008); hence, regression estimates were substituted for annual estimates for 1974-83, with an extrapolation to 1973. These values were 175.6, 176.1, 176.6, 177.1, 177.6, 178.0, 178.5, 179.0, 179.5, 180.0, and 180.5 cm, respectively, for 1973-83. For the southern stock, insufficient data exist to calculate a length at attainment of sexual maturity for individual years, hence the collective value was used for all years (175.0 cm).

Six factors were examined to determine whether annual changes in the above percentages of pregnant females were caused or affected by changing biases in the sampling methods. These factors include 1) geographical provenance, based on two strata (Fig. 1) which roughly correspond to the historical tuna fishing grounds (inside the Commission Yellowfin Regulatory Area, CYRA) and a more recently exploited area (outside the CYRA); 2) the quarter of the year; 3) the length of chase, or the time between sighting the dolphin school and capture (net set); 4) the observer's estimate of the dolphin school size (only available since 1973); 5) the number of dolphins known to have been killed in the set; and 6) the total number of tons of tuna caught in the set.

The selection of these six factors was guided to

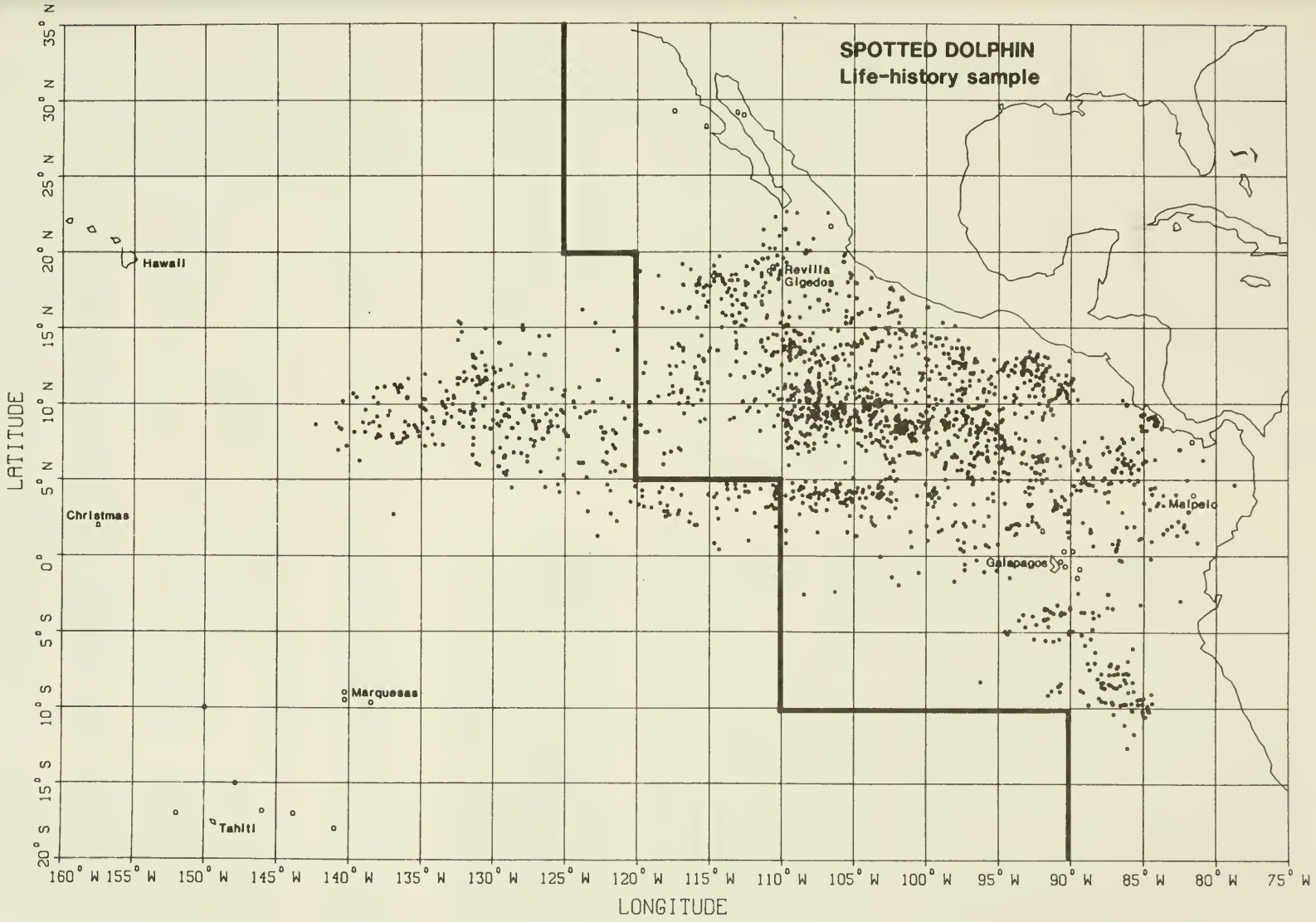

FIGURE 1.—Locations at which male and female spotted dolphins were collected for life history studies, 1968-83. Bold line indicates western border of the Commission Yellowfin Regulatory Area (CYRA). Figure taken from Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass. 1984. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Admin. Rep. LJ-84-02, available from NOAA, Southwest Fisheries Center, La Jolla, CA 92038.

some extent by previous studies. The sex ratio and the fraction of yearling dolphins in a sample were found to vary with kill size (No. 5 above). The fraction of neonatal animals in tuna-vessel samples was found to vary significantly with area, season, chase time, dolphin kill, and tuna catch (Nos. 1, 2, 3, 5, and 6 above)[3]. Preliminary work by A. A. Hohn[4] and M. D. Scott[5] has indicated that immature spotted dolphins may segregate into schools with different characteristic school sizes (No. 4 above).

The significance of each of the above factors was tested separately using a Pearson chi-square. For each test, the null hypothesis was that either percent pregnant, percent lactating, or percent mature is independent of the factor being tested. If this hypothesis is shown to be false, then it is likely that reproductive parameters may be affected by sampling bias. Unfortunately, the above sampling factors are not independent; a factor may appear significant when, in fact, that factor is merely correlated with a causative factor. Because of this, probablilties should be interpreted with caution.

Multiway comparisons were used to discriminate factors which are truly important from those which are correlated to significant factors. A hierarchical approach was used, based on the log-linear model for discrete multivariate analysis (program BMDP4F, Dixon 1981). The above 2-way tests were used to identify factors that may be significant. The factors that were significant in the 2-way tests were used in 3-way tests. The factors which proved significant in the 3-way tests were then included in 4-way tests (which proved to be a practical upper limit on multiway tests using our data set). In this manner, multiway comparisons of factors could be tested, whereas a 7-way test of all factors would not have been feasible.

Analysis of variance (ANOVA) was tried and rejected as an alternative to the log-linear model for multiway comparisons. The method used in this trial was to calculate percent pregnant for each set and to use sets as replicates in an ANOVA. Although ANOVA is recognized to be robust to violations in assumptions, the sample size for individual sets is very small (mean number of mature females per set is 1.6, mode is 1). As a result, the percent pregnant in 72% of sets was either 0% or 100% of mature females. No transformation was able to normalize these data. Using an arc-sine transformation, 2-way ANOVA was not even able to recognize the four significant factors affecting percent pregnant that were identified using a simple Pearson chi-square. Because of these problems, the ANOVA model was rejected for use in the multiway comparisons.

RESULTS

Percent Pregnant

The fractions of sexually mature females that were pregnant are given in Table 1 for the samples of the northern and southern offshore stocks collected from 1971 to 1983. Sample sizes decline in the later years for the northern stock, but are typically >100.

[3]Powers, J. E., and J. Barlow. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Doc. SOPS/79/31, 7 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[4]A. A. Hohn, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

[5]M. D. Scott, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038, pers. commun. November 1983.

TABLE 1.—Fractions a) of females that were sexually mature, b) of sexually mature females that were pregnant, and c) of pregnant females that were lactating. Samples include 1971-83 specimens from the northern and southern offshore stocks of spotted dolphins. Fraction mature was not sampled in 1971 and 1972.

	Year													
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	Overall
Northern stock														
a) Fraction mature			0.56	0.53	0.54	0.50	0.61	0.59	0.59	0.55	0.61	0.56	0.50	0.561
Number in sample			1,149	1,013	1,215	751	995	564	593	509	465	579	137	7,970
b) Fraction pregnant	0.48	0.41	0.42	0.29	0.29	0.34	0.27	0.24	0.30	0.30	0.29	0.32	0.38	0.329
Number mature	79	449	573	487	493	291	375	229	205	148	153	148	37	3,667
c) Fraction lactating	0.26	0.08	0.08	0.17	0.14	0.13	0.35	0.15	0.30	0.23	0.24	0.19	0.28	0.162
Number pregnant	38	180	236	138	130	93	94	52	61	43	42	47	14	1,168
Southern stock														
a) Fraction mature			0.58	—	0.68	0.63	0.61	0.77	0.58	0.73	0.60	0.70	0.69	0.656
Number in sample			24	0	38	254	23	51	166	59	20	199	106	940
b) Fraction pregnant	—	—	0.75	—	0.49	0.48	0.12	0.28	0.22	0.35	0.00	0.32	0.18	0.364
Number mature	0	0	12	0	23	145	8	25	60	17	8	73	22	393
c) Fraction lactating	—	—	0.00	—	0.22	0.04	0.00	0.16	0.08	0.00	—	0.23	0.00	0.087
Number pregnant	0	0	9	0	9	68	1	6	13	6	0	22	4	138

Samples sizes for the southern stock are highly variable between years, and several years have too few specimens to reliably estimate the fraction of the population that would be pregnant. For 1973-83, the overall percentage of pregnant females is, however, significantly higher for the southern stock, 36.4%, than for the northern stock, 31.4% (χ^2_1 = 3.97, P = 0.05). Because of this difference, northern and southern stocks were not pooled in subsequent analyses. Due to the small sample size from the southern stock, examination of trends and biases in female reproductive rates was limited to the northern stock.

Annual estimates of the percentage of pregnant females are illustrated in Figure 2 for the northern offshore stock. The regression is significant; however, the residuals do not appear randomly distributed. The negative slopes of the regression lines are largely due to high pregnancy rates in 1971-73. Expected values for the percent pregnant in each year were generated in two ways: from the overall percent pregnant and from the "de-trended" regression predictions. Chi-square tests using these expected values show the annual variability in percent pregnant is greater than would be expected from random sampling of a population with a constant ($P < 0.001$) or linearly decreasing ($P < 0.001$) pregnancy rate.

Although natural year-to-year variability in pregnancy rates cannot be ruled out, a changing bias in sampling could also cause larger than expected variability in percent pregnant. To look for such a bias, the sample from the northern stock was stratified by the six sampling factors described above. The percent pregnant in each of these strata is given in Table 2, with the chi-square probabilities that the samples could have been drawn randomly from the pooled sample. Of the factors examined, pregnancy rate was significantly related to sampling season, dolphin kill-per-set, and tuna catch-per-set (henceforth the latter two are referred to as kill and catch).

Because sampling seasons, mean dolphin kills, and mean tuna catches vary significantly between years, these factors cannot be considered independent of year. For instance, the interaction between pregnancy rates and dolphin kill might appear significant due to high kill rates or high catch rates in a year (or years) that coincidentally had high pregnancy rates. Conversely, high pregnancy rates in one year may be due to a sampling bias related to dolphin kill.

Multiway tests were used to identify possible interactions between the three significant factors and year effects. In all cases, 3-way tests indicate that year effects are significant (Table 3). First order effects of kill, catch, and season were not significant; however, higher order effects involving the latter two were important (Table 3). A 4-way test using catch, season, and year also shows significant higher order interactions involving both catch and season (Table 3).

Higher order interactions involving year and another factor indicate that effect of that factor changes with year. Since pregnancy rates appear to have changed markedly from 1971-73 to 1974-83 (Fig. 2), the effect of the significant factors was

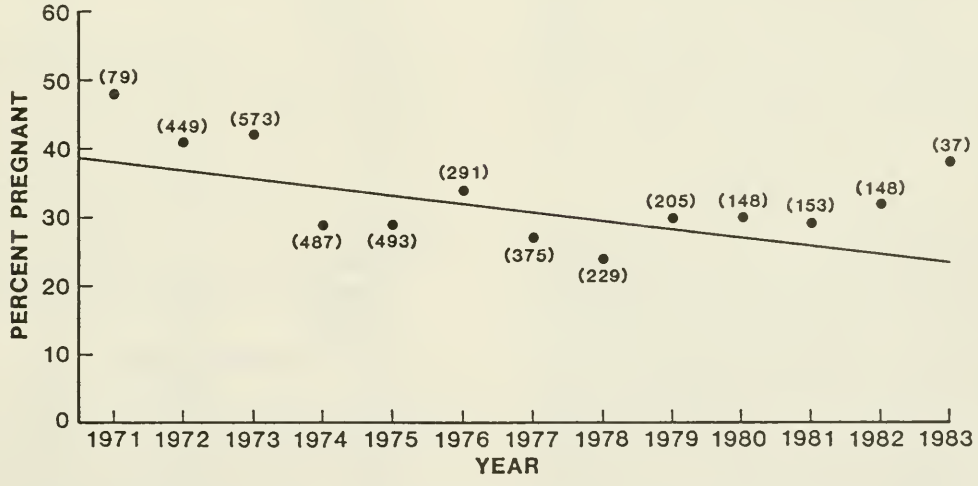

FIGURE 2.—Percentages of mature females that were pregnant for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid line represents weighted regression. Sample sizes are in parentheses.

TABLE 2.—Percentage of sexually mature females that were pregnant (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Pregnant (%)	*N*	Probability
1) Geographic area			
Inside CYRA	33.5	3,032	0.09
Outside CYRA	30.0	633	
2) Season			
1st quarter	34.7	1,799	
2d quarter	33.5	741	0.04
3d quarter	28.9	584	
4th quarter	30.4	542	
3) Chase time (min)			
<20	31.2	1,081	
20-40	34.8	1,440	0.09
>40	31.1	747	
4) School size			
<500	30.2	443	
500-1,500	29.8	741	0.49
>1,500	27.4	693	
5) Number killed			
1-10	29.8	1,104	
11-30	30.1	917	<0.001
>30	37.4	1,301	
6) Tuna caught (tons)			
0-5	29.0	428	
6-15	33.0	848	0.02
16-30	30.4	760	
>30	35.6	1,280	

tested separately for these two time periods. When the years 1971-73 were excluded (Table 4), the interactions between percent pregnant and season, dolphin kill, and tuna catch are no longer significant. When tests are performed on data from 1971 to 1973 alone (Table 4), season and tuna catch are still significantly related to pregnancy rate.

Percent Lactating

Annual trends in percent lactating for the northern stock of spotted dolphins are illustrated in Figure 3. Two cases are considered: 1) the percentage of all mature females that are lactating and 2) the percentage of pregnant females that are lactating. For both cases, a weighted regression shows a significant increase in the fraction of lactating females through time ($P < 0.05$). In the former case, the regression again appears to be driven by anomalous values in 1971-73. Percentages and sample sizes for the latter case are presented in Table

TABLE 3.—Multiway tests of factors affecting percent pregnant. Log-likelihood chi-square was used to calculate the probability that percent pregnant is independent of the stated factor(s) using the log-linear model. Pregnancy state (pregnant/not pregnant) is implicit as the first factor in each comparison.

Tests	Probability
3-way	
a) Year	<0.0001
Season	0.70
Year × season	<0.0001
b) Year	<0.0001
Kill	0.09
Year × kill	0.31
c) Year	<0.0001
Catch	0.14
Year × catch	0.0004
4-way	
Year	<0.0001
Season	0.90
Catch	0.15
Year × season	<0.0001
Year × catch	0.0002
Season × catch	0.003
Year × season × catch	0.07

TABLE 4.—Percentage of sexually mature females that were pregnant, grouped by season, dolphin kill, and tuna catch. The years 1971-73 and 1974-83 are grouped separately. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included.

Year	Pregnant (%)	*N*	Probability
1971-73 overall	41.9	1,101	
Season			
1st quarter	44.0	722	
2d quarter	47.6	210	<0.001
3d quarter	—	0	
4th quarter	25.4	169	
Number killed			
1-10	38.0	171	
11-30	39.5	248	0.23
>30	44.1	651	
Tuna caught (tons)			
0-5	37.6	101	
6-15	44.5	247	0.04
16-30	35.0	226	
>30	45.5	490	
1974-82 overall	29.0	2,566	
Season			
1st quarter	28.4	1,077	
2d quarter	27.9	531	0.39
3d quarter	28.9	584	
4th quarter	32.7	373	
Number killed			
1-10	28.3	933	
11-30	26.6	669	0.27
>30	30.6	650	
Tuna caught (tons)			
0-5	26.3	327	
6-15	28.3	601	0.76
16-30	28.5	534	
>30	29.5	790	

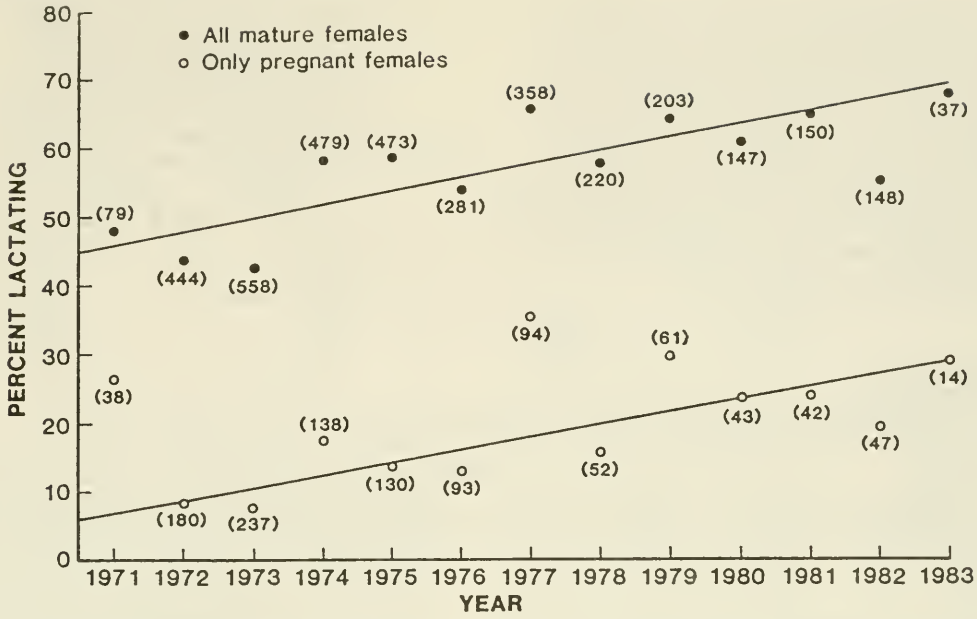

FIGURE 3.—Percentages of mature females that were lactating and percentages of pregnant females that were lactating for the northern offshore stock of spotted dolphins from 1971 to 1983. Solid lines represents weighted regressions. Sample sizes are in parentheses.

1 for both the northern and southern stocks. Again sample size for the southern stock is too small to examine individual years; however, the overall percent of pregnant females that were lactating in 1973-83 samples shows significant differences between stocks ($\chi^2_1 = 6.50$, $P = 0.01$). Annual variability for the northern stock is greater than expected from random sampling of a population with a constant percent lactating ($\chi^2_{12} = 63.5$, $P < 0.001$).

When the sample of pregnant females from the northern stock is stratified by the six sampling factors, lactation state was significantly related to sampling season, dolphin kill, and tuna catch (Table 5). Again, 3-way tests showed that the first order effect of these factors was not significant when year was included as the third factor (Table 6). In each of these cases, the first order effect of year was important. In one case, dolphin kill, a second order interaction between kill and year was also significant.

Percent Mature

The fractions of females that were sexually mature are given in Table 1 by stock and by year (1973-83). Again the sample sizes are sufficient in all years for the northern stock but are inadequate in some years for the southern stock. The southern stock is significantly different from the northern stock in percent mature ($\chi^2_1 = 31.2$, $P < 0.001$), and (given its small sample size) the southern stock was excluded in subsequent stratifications.

The percentage of all females that are mature from 1973 to 1983 is illustrated in Figure 4 for the northern stock. In this case, the weighted regression is not significant. Using chi-square tests, the level of annual variability in percent mature is larger than would be expected from randomly sampling a population with a constant fraction of mature females ($P < 0.001$).

For long-lived animals such as dolphins, annual variability in percent mature should be small and changes in this population parameter should be gradual. Since the annual variability observed in the data is larger than would be expected from random sampling error, year-to-year changes in sampling biases are likely. Percent mature was found to be significantly related to three of the six sampling factors examined: sampling season, dolphin kill-per-set, and tuna catch-per-set (Table 7).

Each of these three significant factors was tested with maturity state and year using 3-way tests (Table 8). For each of these factors, year was a significant factor and all other first order effects were not significant. Only dolphin kill showed a significant second order interaction with year.

TABLE 5.—Percentage of pregnant dolphins that were lactating (1971-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Lactating (%)	*N*	Probability
1) Geographic area			
Inside CYRA	15.7	988	0.30
Outside CYRA	18.8	181	
2) Season			
1st quarter	11.9	611	
2d quarter	17.2	239	<0.001
3d quarter	26.7	161	
4th quarter	20.3	158	
3) Chase time (min)			
<20	14.8	331	
20-40	14.0	479	0.27
>40	18.6	226	
4) School size			
<500	20.0	130	
500-1,000	18.0	211	0.87
>1,500	19.7	183	
5) Number killed			
1-10	19.1	319	
11-30	16.5	267	0.03
>30	12.3	471	
6) Tuna caught (tons)			
0-5	20.5	117	
6-15	16.4	275	0.17
16-30	16.7	221	
>30	12.8	444	

TABLE 6.—Multiway tests of factors affecting the percentage of pregnant females that are lactating. Log-likelihood chi-square was used to calculate the probability that percent lactating is independent of the stated factor(s) using the log-linear model. Lactation state (lactating/not lactating) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	<0.0001
Season	0.29
Year × season	0.007
b) Year	<0.0001
Kill	0.79
Year × kill	0.51

TABLE 7.—Percentage of female dolphins that were sexually mature (1973-83) grouped by 1) the area in which the specimens were collected; 2) the quarter of the calendar year; 3) the length of time between sighting the school and release of the net; 4) the observer's estimate of the total school size; 5) the number of dolphins known to be killed in the set; and 6) the tons of tuna caught in the set. Note that total sample size varies with the availability of data on the stratifying variable. Probabilities are based on chi-square contingency tests. Only samples from the northern offshore stock of spotted dolphins are included. CYRA = Commission Yellowfin Regulatory Area.

	Mature (%)	*N*	Probability
1) Geographic area			
Inside CYRA	55.7	6,329	0.19
Outside CYRA	57.5	1,625	
2) Season			
1st quarter	54.2	3,495	
2d quarter	57.2	1,738	0.02
3d quarter	58.2	1,580	
4th quarter	57.6	1,155	
3) Chase time (min)			
<20	54.4	2,067	
20-40	56.1	3,084	0.36
>40	56.5	1,689	
4) School size			
<500	53.5	1,183	
500-1,500	56.8	1,970	0.19
>1,500	56.0	1,753	
5) Number killed			
1-10	57.9	2,465	
11-30	54.9	2,068	0.02
>30	54.0	2,321	
6) Tuna caught (tons)			
0-5	53.3	920	
6-15	55.1	1,779	0.05
16-30	54.5	1,668	
>30	57.7	2,482	

DISCUSSION

Changes in the reproductive status of the female segment of a population can be monitored using a variety of reproductive indices: 1) mean age at sexual maturation, 2) mean length (or weight) at sexual maturation, 3) annual pregnancy rates, 4) calving interval, 5) percentage of mature females that are pregnant, 6) percentage of females that are lactating, and 7) percentage of females that are sexually mature. Changes in each of these are examined below.

Changes in Maturation Parameters

Myrick et al. (1984) have found no significant difference in the age at sexual maturation (ASM) between a sample from 1973 to 1978 and another sample from 1981. In the present study, length at attainment of sexual maturity is estimated to have increased 4.4 cm from 1974 to 1983. If these results hold, dolphins must be growing faster in recent years. Given small sample sizes of aged individuals, significant changes in ASM may be difficult to detect. Previous studies have shown that the age at sexual maturation is quite responsive to population changes in marine mammals (Fowler 1984), while length at maturation tends to show little change. For fin whales, *Balaenoptera physalus*, Lockyer (1972)

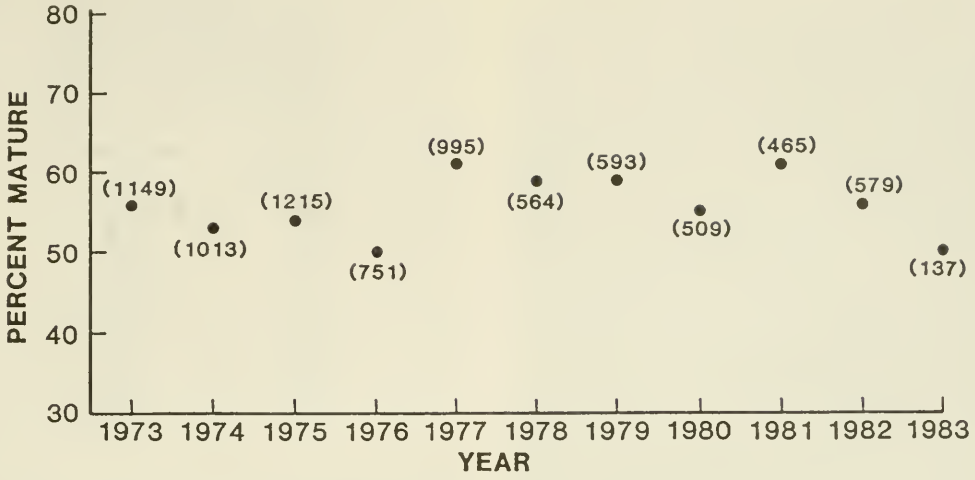

FIGURE 4.—Percentages of all females that were mature for the northern offshore stock of spotted dolphins from 1971 to 1983. Sample sizes are in parentheses.

TABLE 8.—Multiway tests of factors affecting percent mature. Log-likelihood chi-square was used to calculate the probability that percent mature is independent of the stated factor(s) using the log-linear model. Maturation state (mature/not mature) is implicit as the first factor in each comparison.

3-way tests	Probability
a) Year	0.003
Season	0.49
Year × season	0.08
b) Year	0.003
Kill	0.16
Year × kill	0.002
c) Year	0.0009
Catch	0.09
Year × catch	0.42

showed a decrease in ASM without any change in the length at which maturity is attained. Laws (1956) predicted an inverse relationship between ASM and early growth rates for marine mammals. Spotted dolphins appear to show an increase in length at maturation with no change in ASM, and thus do not follow predicted patterns.

Trends in Percent Pregnant

Annual pregnancy rates, calving interval, and percent pregnant all measure essentially the same thing. Annual pregnancy rate and calving interval require knowledge of gestation times. Because density compensatory responses have not been shown in cetacean gestation times, it is more straightforward to deal directly with percent pregnant.

What appeared to be a rapid decline in dolphin pregnancy rates from 1973 to 1978 (Henderson et al. fn. 2), now appears as two eras with distinctly different pregnancy rates. The fraction of pregnant females in the 1971-73 samples was quite high. The 10 years since 1973 show a lower and relatively constant fraction of pregnant females. This difference in results is due largely to use of a larger sample size and a longer time series.

There is no evidence of the sort of slow, long-term trends in pregnancy rates that might be associated with changes in population sizes. The reason for the dramatic change in pregnancy rates between 1973 and 1974 is not known. At least three hypotheses could be used to explain this change: 1) it was the result of a naturally high pregnancy rate in 1971-73; 2) it was the result of heavy fishing-related mortality of nursing calves prior to 1974 that resulted in artificially high pregnancy rates; or 3) it was the result of a bias in the sampling by tuna vessels.

The first hypothesis suggests that changing environmental conditions result in annual changes in pregnancy rates. In the ETP the largest environmental perturbations are associated with "El Niño" events which occur on the time scale of from 5 to 10 yr (Rasmusson and Carpenter 1982). El Niño conditions prevailed in 1972 (moderate), 1975-76 (weak), and 1982-83 (very strong). These dates do not help explain the change in pregnancy rates that occurred between 1973 and 1974.

The second hypothesis is that heavy dolphin mortality in the 1960's and early 1970's may have somehow affected dolphin pregnancy rates. Large reduc-

tions in dolphin mortality occurred following the passage of the Marine Mammal Protection Act of 1972 (Table 9). If mortality rates were higher for nursing calves, calving interval might have been shortened. This would result in higher pregnancy rates and lower lactation rates, both of which were observed in 1971-73. Analyses have indicated that very young calves are more susceptible to tuna-net mortality (Powers and Barlow fn. 3; Stuntz[6]). Indirectly, high calf mortality may also result from the separation of a calf from its mother during long chases. It is not known if the magnitude of these effects could have resulted in the observed changes in pregnancy or lactation rates.

The third hypothesis is that sampling methods were somehow different between 1971-73 and 1974-83. The only difference in the sampling design was that in 1971-73, scientific technicians were placed only on tuna vessels that agreed to cooperate. Beginning in 1974, the selection of vessels was random. It is difficult, however, to see how this change would affect the percent pregnant in the samples. As was noted above, percent pregnant was significantly correlated with sampling season, dolphin kill-per-set, and tuna catch-per-set during the years 1971-73, but not during the years 1974-83. The reason for this difference is not known, but this would seem to be evidence that sampling was more random in the latter period.

The observed change in percent pregnant from 1971-73 to 1974-83 cannot be explained with certainty. The high pregnancy rates in 1971-73 can be logically explained by direct or indirect effects of the fishery or by sampling biases in those years (Hypotheses 2 and 3). Determining whether either (or both) hypothesis is true may not be possible with existing data.

Trends in Percent Lactating

Changes were also found in the percentage of lactating females. For mature females, the fraction lactating shows low values in 1971-73 and high values in 1974-83, which is opposite the pattern seen for fraction pregnant. This inverse correlation would be expected given that pregnancy state and lactation state are physiologically linked (i.e., cessation of lactation leads to ovulation and pregnancy). Perhaps more meaningful is the increase in the fraction of pregnant females that were lactating. Because being simultaneously pregnant and lactating represent the greatest energy drain on female dolphins, this quantity is likely to be very sensitive to changes in environmental conditions. Because nonpregnant females are excluded, this quantity should also be insensitive to sample biases that are related solely to pregnancy state.

Given that no trends were seen in the percent pregnant from 1974 to 1983, we can infer that the calving interval, or the mean period between births for a mature female, also did not change during that time. If calving interval were constant, the increase in the fraction of pregnant females that were lactating indicates that females may be nursing their calves for a longer period of time, hence a longer lactation period. This increase in the lactation period may have resulted from a decrease in fishery related calf mortality during the 1971-83 period. Because calves may be more susceptible to death or separation from their mothers during the chase, capture, and release of a dolphin school, mean lactation periods may have been abbreviated during the earlier years (Hypothesis 2 above).

TABLE 9.—Estimates of numbers of spotted dolphins killed by all purse seine vessels in the eastern tropical Pacific, 1968-78 (data from Smith 1983).

Year	Spotted dolphins killed
1968	178,000
1969	365,000
1970	355,000
1971	176,000
1972	288,000
1973	131,000
1974	95,000
1975	105,000
1976	47,000
1977	22,000
1978	19,000

Trends in Percent Mature

No significant trends in the percentage of females that were sexually mature during 1971-83 are evident for the northern stock of spotted dolphins. Annual variability was far too great to be explained by random sampling error. This parameter showed a significant correlation with dolphin kill-per-set. Therefore, unless sampling conditions remain constant (which they have not), percent mature is not a useful index for monitoring reproductive capability of the spotted dolphin populations.

[6]Stuntz, W. E. 1980. Variation in age structure of the incidental kill of spotted dolphins, *Stenella attenuata*, in the U.S. tropical purse-seine fishery. Admin. Rep. LJ-80-06, 29 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

Variability in percent mature with sampling conditions may result from several interacting factors. Preliminary data have indicated that spotted dolphins in the ETP may segregate on the basis of reproductive maturity (A. A. Hohn fn. 4 and M. D. Scott fn. 5). Schools that consist principally of immature dolphins may have a smaller characteristic school size, may be less likely to have large numbers of tuna associated with them, and may be more vulnerable to high kills-per-set due to the inexperience of younger dolphins. Also, the consistent underrepresentation of immature age classes in the spotted dolphin age distribution (Barlow and Hohn 1984) indicates that a very significant bias may occur in the sampling of immature animals. These are largely speculations, and until a well-supported explanation for sampling variability is presented and until some method of removing this bias is found, percent mature should not be used as an index of changes in spotted dolphin reproduction.

Gross Annual Reproductive Rate

Changes in GARR have been used as a measure of changes in the net rate of growth for a population (Smith 1983). This approach has been faulted on the basis that it does not consider age structure effects (Polacheck 1982), and more critically on the basis that such an approach is theoretically unsound (Goodman[7]). These criticisms do not, however, detract from the usefulness of GARR as an index of gross per capita reproduction for a population.

If GARR were robust to sampling conditions, it could be one of the most useful indices of population reproduction. One advantage is that a GARR index considers percent pregnant and percent mature simultaneously, and hence compensatory changes in these two do not affect the index. Simply stated, GARR is calculated as (the fraction of females in a population) × (the fraction of females that are mature) × (the fraction of mature females that are pregnant)/(gestation time). Unfortunately, percent mature is a major component in these calculations, and this parameter has been found to be dependent on sampling conditions. Until sampling problems associated with estimating percent mature are resolved, GARR is not likely to be a useful index of change in reproductive rates.

Between-Population Comparisons

The northern and southern stocks of spotted dolphins have been subjected to very different levels of fishing-related mortality. Smith[8] has estimated the northern stock to be at 38-55% of its 1959 level and the southern stock to be at 93-98% of its historical level. Density dependent increases in reproductive rates might be predicted for the northern stock relative to the southern stock.

The percentage of mature females that were pregnant differs significantly between the northern and southern stocks. Surprisingly, however, the southern stock was found to have the higher percent pregnant (36% vs. 33%). Another exploited population of spotted dolphins in the western Pacific was found to have an annual pregnancy rate of 0.254 (Kasuya 1976), which (with a gestation time of 11.2 mo) would give an average percent pregnant of about 24%. Considerable variability in percent pregnant can thus exist between spotted dolphin populations, none of which is obviously related to density compensatory effects. Sampling of the southern population has, however, been sporadic, and if annual variability in pregnancy rates is greater for that stock, a few years' data may not be sufficient to accurately estimate a long-term mean. Nonetheless, the tendency for a more exploited stock to have lower reproductive rates is worrisome, and future life history comparisons between the northern and southern stocks would probably be useful.

Evidence for density compensatory changes in pregnancy rates were also lacking when two spinner dolphin, *S. longirostris*, populations were compared (Perrin and Henderson 1984). They found similarly that the more heavily exploited stock (eastern spinners) had a lower percent pregnant than the less heavily exploited stock (whitebelly spinners). The opposite would be predicted based purely on density compensatory effects.

The overall percentage of pregnant females that are lactating is significantly higher for the northern spotted dolphins than for the southern stock. The biological significance of this result is questionable given the year-to-year variability in this parameter. Between-population comparisons of this percentage are not likely to be meaningful until the cause of this large annual variability is identified.

As was noted above, the percentage of females that

[7]Goodman, D. 1984. Uses of the gross annual reproduction rate calculation in the dolphin assessment. Admin. Rep. LJ-84-22C, 17 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[8]Smith, T. D. (editor). 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). Admin. Rep. LJ-79-41, 120 p.; available from Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

are mature also appears to be higher in the southern stock than in the northern stock. Given the dependence of this parameter on sampling conditions, little confidence should be placed on this result. The direction of the difference (more immatures in the northern population) is consistent with a higher population growth rate in the north. Work is in progress to determine whether this difference could be due to differences in the age at sexual maturation (Myrick[9]).

No data exist yet on the mean age at sexual maturation for females in the southern stock. As mentioned in the Methods section, data do exist on the "length at sexual maturation" for both the northern and southern stocks. For the northern stock, this length appears to have increased from 176 cm in 1974 to 181 cm in 1983. For the southern stock this length was estimated as 175 cm from the pooled 1974-83 data. The length at sexual maturation is greater for the northern stock, which is consistent with the greater mean asymptotic length of the northern specimens (Perrin et al. 1979).

CONCLUSION

My intent in writing this paper was to identify indices that may be of value in monitoring the reproductive health of spotted dolphins in the eastern Pacific. Two of the indices that were examined (the percentage of mature females that are pregnant and the percentage of pregnant females that are lactating) are likely to be useful for this purpose. Both are relatively insensitive to sampling biases, and both measure important aspects of the female reproductive cycle. Problems exist in measuring the fraction of females that are mature. This parameter is also an important index of net reproduction in a population. It is possible that a stable index of percent mature could be obtained using some stratification scheme. A first approach might be to examine finer scale geographic differences in percent mature. Additional work is necessary before significance can be ascribed to between-population differences in percent mature.

ACKNOWLEDGMENTS

Much credit is deserved by the many technicians who gathered the data upon which this report is based. Their labors were often under very difficult working conditions. I also wish to thank the data editing and managing group and the graphics department, SWFC. Ideas presented in this manuscript were largely generated in discussions with A. Hohn and W. Perrin. The current draft of this manuscript benefited greatly from critical reviews by J. Bengtson, D. Chapman, D. DeMaster, F. Hester, A. Hohn, J. Mean, A. Myrick, W. Perrin, S. Reilly, and G. Sakagawa.

[9]A. C. Myrick, NOAA, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1984.

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ANNUAL BAND DEPOSITION WITHIN SHELLS OF THE HARD CLAM, *MERCENARIA MERCENARIA*: CONSISTENCY ACROSS HABITAT NEAR CAPE LOOKOUT, NORTH CAROLINA

The presence of periodically repeating features in the preservable hard parts of various organisms allows scientists in several disciplines to make important inferences about the rates and timing of past events (Jones 1980; Rhoads and Lutz 1980). Analysis of growth lines deposited in shells of bivalve molluscs, for example, finds powerful application in the fields of paleontology (Rosenberg and Runcorn 1975), anthropology (Clark 1979), population ecology (Kennish 1980), and fisheries biology (Peterson et al. 1983). Possession of a reliable age marker in a bivalve shell enables fisheries biologists 1) to construct age-frequency distributions for various populations, which reflect the age-specific mortality rates and help permit estimates of sustainable yield, 2) to calculate individual growth rates and their variability among habitats, and 3) to understand age-specific reproductive schedules in exploited populations.

Unfortunately, the potential rewards in applying this aging technique have encouraged widespread use of growth line analysis prior to performing the necessary controls to test the annual periodicity of line deposition (Clark 1974; Gould 1979; Jones 1981). Because of the tremendous potential utility of this aging technique, we carried out mark-recapture tests of the annual nature of growth band deposition in shells of the commercially important hard clam, *Mercenaria mercenaria*, in a North Carolina sound (Peterson et al. 1983). Although these experiments provided convincing evidence that *M. mercenaria* deposits a reliable annual marker in the form of an internal summer growth band in its shell, this study was carried out in only a single locality in Back Sound, NC. Patterns of growth band deposition in bivalve molluscs may vary with environment on several scales: 1) over a broad geographic scale, *M. mercenaria* deposits summer bands in Back Sound, NC, and in Chesapeake Bay, but winter bands in all localities in northeastern states (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Kennish and Olsson 1975; Clark 1979; Clark and Lutz 1982; Fritz and Haven 1983; Peterson et al. 1983); 2) among habitats within estuaries, *Protothaca staminea* appears to deposit unambiguous annual bands in muddy sand but not in a clean-sand habitat in Mugu Lagoon, CA (Peterson and Ambrose 1985); and 3) among nearby individuals within a single habitat, both *Chione fluctifraga* and *Protothaca staminea* from within the same restricted sample at Mugu Lagoon exhibit radically different patterns of daily line deposition (Hughes and Clausen 1980). We present here results of additional tests of the annual nature of internal growth band deposition in shells of *M. mercenaria* placed for 2 yr in several different field localities and estuarine habitats, in order to test whether our earlier (Peterson et al. 1983) demonstration of annual banding in North Carolina's *M. mercenaria* is robust to change in local habitat.

Materials and Methods

To extend the generality and power of our previous results, we designed a mark-recapture experiment to examine the frequency and clarity of band deposition in *M. mercenaria* at 5 additional sites (Fig. 1) within Carteret County, NC, near Cape Lookout. These sites were chosen to represent a wide geographic spread among several local water bodies, to permit contrasts between vegetated and unvegetated habitats, and to include more sandy (coarse) substrate than that in our original site. One site was selected on a fine sand flat in the North River about 12 km from our earlier Middle Marsh study site in Back Sound. Two sites were chosen about 38 km from Middle Marsh near the western end of Bogue Sound by the town of Cape Carteret: one on a fine sand flat and the other in a seagrass bed with mixed stands of *Zostera marina* and *Halodule wrightii*. The other two sites were situated in Core Sound about 6 km from Cedar Island Point and about 47 km from our initial Middle Marsh study site: one on a sand flat and the other in a *Halodule wrightii* meadow. All sites were on shallow subtidal bottom, accessible by wading and amenable to recovery of marked animals.

Table 1 summarizes the results of particle-size analyses done on duplicate surface (0-5 cm) sediment cores taken in August-September 1981 at each site to permit comparisons among the five new and one previous study sites. The five new sites are clearly characterized by having much coarser sediments than the previous study site but differ among themselves in sediment grade (Table 1). Contemporaneous

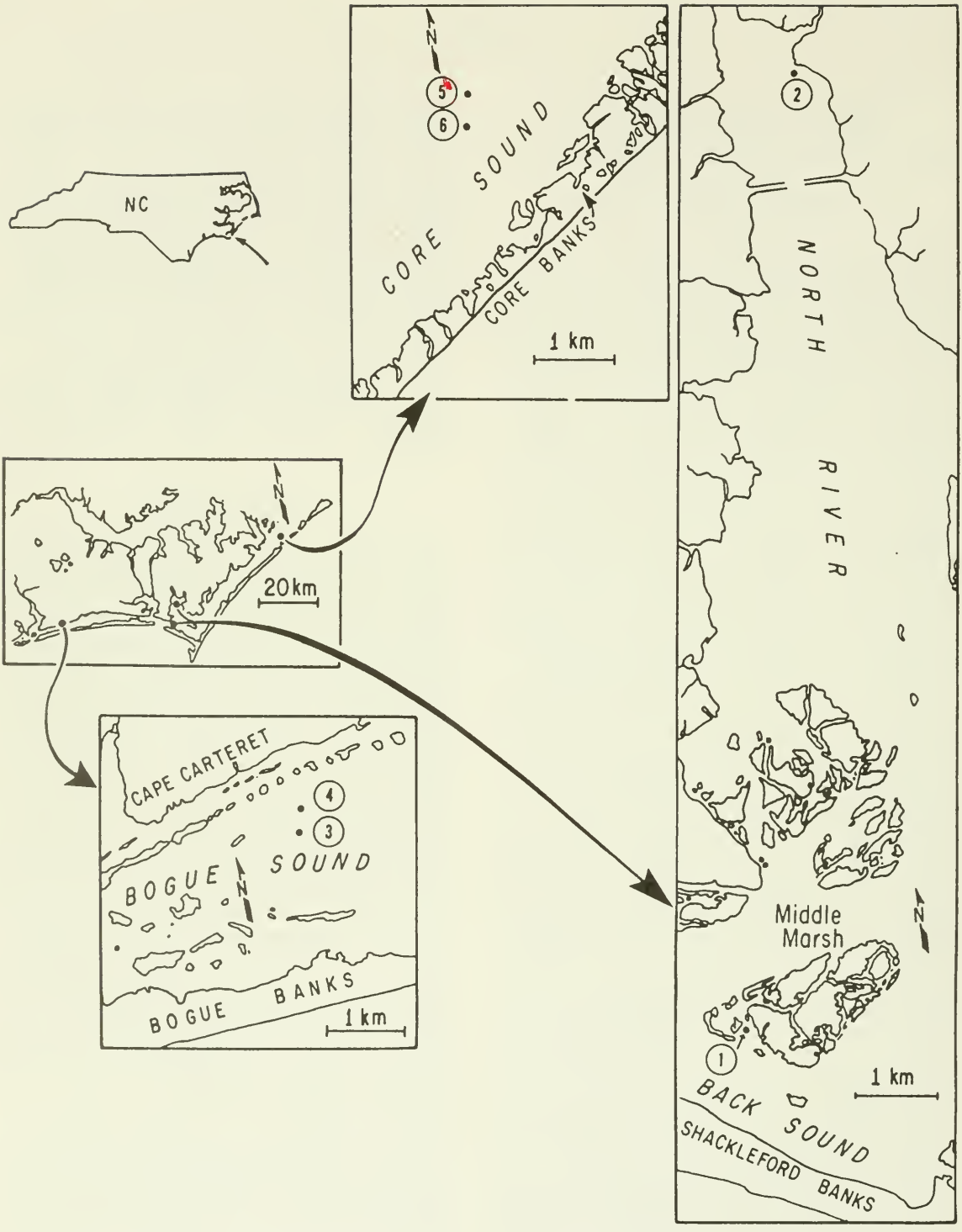

FIGURE 1.—Geographic locations of study sites (marked by dots near circled numbers) within North Carolina near Cape Lookout (marked by the arrow on the NC map): the previous site at Middle Marsh (1); new sites at North River (2); Bogue Sound sand (3) and seagrass (4); Core Sound sand (5) and seagrass (6).

TABLE 1.—Locations and sedimentary characteristics of the one previous (Middle Marsh) and five new study sites of *Mercenaria mercenaria*. Sedimentary data came from seiving and pipetting (Folk 1974) duplicate surface (0-5 cm) sediment cores taken in summer 1981 at each site. Percent silt-clay is percent of total sediment dry weight in fine (>4Φ) size classes.

Site	Location coordinates	Mean sediment parameters (±SD)		
		Graphic mean	Percent silt-clay	Sorting coefficient
Middle Marsh in Back Sound	34°41′28″N 76°37′03″W	5.07 (0.28)	47.22 (12.24)	3.00 (0.51)
North River	34°48′22″N 76°36′48″W	2.35 (0.02)	2.97 (1.72)	0.61 (0.01)
Bogue Sound Sand	34°41′29″N 76°59′06″W	2.83 (0.09)	2.15 (0.05)	0.47 (0.02)
Bogue Sound Seagrass	34°41′36″N 76°59′05″W	3.05 (0.02)	9.31 (2.22)	0.95 (0.17)
Core Sound Sand	34°57′03″N 76°12′44″W	2.72 (0.07)	8.81 (2.03)	0.91 (0.16)
Core Sound Seagrass	34°56′59″N 76°12′43″W	2.40 (0.00)	3.10 (1.33)	0.60 (0.06

water temperature and salinity data are not available for all sites, but records from a variety of sources (Brett 1963; Thayer 1971; Williams et al. 1973; Sutherland and Karlson 1977; H. J. Porter, University of North Carolina, Chapel Hill, unpubl. data; W. Kirby-Smith, Duke University, unpubl. data) suggest that 1) water temperature patterns probably do not differ greatly across sites, with monthly averages ranging from winter minima of 2°-4°C to summer maxima of 29°-30°C, and 2) that salinities are slightly more variable across sites. Localities close to Atlantic Ocean inlets (Bogue Sound sand and seagrass sites and the previous Back Sound site at Middle Marsh) experience uniformly high salinities (30-36‰), except after severe rainstorms (Brett 1963; H. J. Porter, unpubl. data). Salinities in the upper portion of North River are only slightly lower because there is little freshwater inflow into that system (Thayer 1971). The lowest (22-28‰) and probably most variable salinities on a week-to-week scale occur at the two Core Sound sites, where exchange with the ocean is reduced and where any persistent north winds bring intrusions of low-salinity waters from Pamlico Sound (Williams et al. 1973).

At each of the five new study sites, we placed groups of 80 *Mercenaria mercenaria* in 1 m^2 field plots in late summer 1980, excavated them by hand in late summer 1981 to estimate growth and mortality and to replace missing and dead clams, and then finally recovered all living clams present in late summer 1982 (Table 2). All *M. mercenaria* used in these experiments were individually marked on the external shell surface with color-coded dots of Mark-Tex Corporation paints and measured initially and at both yearly samplings by calipers to the nearest 0.1 mm in each of three mutually perpendicular dimensions (length, height, thickness). Clams used in these mark-recovery experiments were chosen to reflect a size range from 1 to 10 cm in length. Before placing the marked and measured clams into the field plots, we first installed fences of 6 mm mesh plastic (VEXAR[1]) around the 1 m^2 plots. These fences were identical to those used and described previously (Peterson et al. 1983) and were designed to inhibit emigration and to mark off bottom plots to improve our ability to recover the marked clams. At the three unvegetated sites, we removed all initially present *M. mercenaria* and other large macrofauna before adding marked clams by first using fingers to plow systematically the top 10 cm of sediments and then twice systematically sieving in situ through 6 mm mesh the entire 1 m^2 surface to that same 10 cm depth. This procedure was not used at the initiation of the experiment at the two seagrass sites because it would have removed the seagrass itself. This same procedure was employed, although using a 3.2 mm mesh, at both yearly samplings to recover all marked clams from all 1 m^2 plots at each unvegetated site. At the two seagrass sites, marked clams were recovered by using a hydraulic suction dredge and collecting the contents of the top 15 cm on a 3 mm nylon mesh bag (see Peterson et al. 1983 for data on sampling efficiency of this device). Because of the removal of seagrasses, the locations of all seagrass plots were then shifted slightly (<3 m) to new, undisturbed positions for the second and final year.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Dates of experiment initiation and subsequent sampling of *Mercenaria mercenaria* for each of the five study sites.

Site[1]	Measuring dates		
	1980 initiation	1981 sampling	1982 termination
North River	6 August	30 July	2 August
Bogue Sound Sand	15 August	2 September	24 August
Bogue Sound Seagrass	15 August	24 August	24 August
Core Sound Sand	3 September	9 September	3 September
Core Sound Seagrass	3 September	11 September	3 September

[1]Each site held 1 m^{-2} enclosures of *Mercenaria mercenaria* at 80 m^{-2}: one enclosure contained clams derived from a common Back Sound site (supplemented by 10-20 mm clams from other Back Sound origins), and at least one other enclosure contained only locally derived clams.

At each site, all *M. mercenaria* in these experiments >20 mm in initial length came from one of two different sources. One enclosure at each site held clams planted at the constant density of 80 m^{-2} and collected initially from a single source, a seagrass bed along the southern shore of Back Sound (described in Peterson et al. 1984). One or two additional enclosures held clams collected locally at the specific study site, but again kept at the same 80 m^{-2} density. Low availability of clams in the 10-20 mm size class from the Back Sound source forced us to add hatchery-reared clams (spawned from Back Sound individuals) and wild-caught clams from Middle Marsh also in Back Sound to represent the 10-20 mm sizes in the "common source" enclosure at each site. This smallest size class was available locally at each site to complete the "local-origin" enclosures. This design was chosen to enable us to test whether there were any effects of clam origin (the single Back Sound source vs. local clams) at each of the five study sites.

Upon termination of the experiment almost exactly 2 yr after initial planting of the marked clams (Table 2), subsets of those clams that had survived the complete 2-yr period were selected from each origin treatment at each study site in as wide a range of sizes as possible. These clams were returned to the laboratory and killed by steaming. One valve from each of these 2-yr survivors was then sectioned, using a diamond blade on a slow-speed Buehler ISOMET saw, from umbo to ventral margin along the axis of greatest growth. The shell sections were sanded and polished when necessary to enhance the clarity of natural banding patterns. Because the initial size in August-September 1980 and the intermediate size 1 yr later were known for each of the marked individuals and could be marked on the shell surface, and because the marking and measuring process itself almost invaribly induces deposition of a disturbance check which serves as a very precise internal shell marker (Peterson et al. 1983), we were then able to count with the unaided eye the number of additional growth bands deposited in the internal shell matrix of each clam during its final 2 yr of life. We also observed where these bands were deposited relative to the known sizes at the initial, intermediate, and final measuring dates. These observations permit a test of whether the reliability of using summer growth bands to age North Carolina's *M. mercenaria* varies with site (habitat) or clam origin in the vicinity of Cape Lookout.

Results

We sectioned shells from a total of 89 *M. mercenaria* collected alive in August-September 1982 and known by their paint codes to have been present in the field since the experiment's initiation 24 mo before (Table 2). Of these 89 individuals, 17 either exhibited insufficient growth to permit an accurate determination of the precise shell size at the experiment's initiation or else lacked a disturbance check to mark the precise size at initiation. Of the remaining 72 individuals, all but 2 deposited exactly 2 additional dark growth bands in the final 24 mo of life (Table 3). This pattern was consistent across all five study sites and did not change as a function of clam origin (Table 3). The appearance of the dark

TABLE 3.—For each of five new study sites: 1) numbers of hard clams cut for growth analysis from each origin treatment, 2) numbers of those with insufficient growth to assess band deposition accurately, 3) range of initial clam lengths for those clams with sufficient growth, and 4) average number of bands deposited in the 2-yr experimental period.

	Clam origin							
	Back Sound				Local site			
Study site	No. cut	No. with insufficient growth	Range in initial length (mm)	Av. no. of annual bands added in 2 yr (±1 SE)	No. cut	No. with insufficient growth	Range in initial length (mm)	Av. no. of annual bands added in 2 yr (±1 SE)
North River	10	1	19-74	2 (±0)	17	1	43-80	1.9 (±0.1)
Bogue Sound Sand	10	1	14-57	2 (±0)	11	2	21-72	2 (±0)
Bogue Sound Seagrass	3	1	39-69	2(±0)	3	1	44-48	2 (±0)
Core Sound Sand	10	0	18-75	2 (±0)	5	3	63-70	2 (±0)
Core Sound Seagrass	10	1	15-72	2 (±0)	10	6	46-56	2 (±0)

band in cross-section was identical to that previously described and illustrated by photograph (Peterson et al. 1983) of clams harvested from the Middle Marsh locality.

The pattern of band deposition relative to times of initial planting, first measurement (12 mo), and collection (24 mo) was also extremely consistent across all data sets. Initial planting in 1980 occurred during the period of annual band deposition for 70 of the 72 clams. (In one clam, the 1980 annual band was just completed and in another the 1980 annual band was just about to begin at the time of initial planting.) The disturbance check caused by the 12-mo measurement fell near the end of the growth band for 70 clams and just after the band for the two others. The time of collection in 1982 fell during or just immediately after the deposition of the 1982 annual band for all clams except those from local origin at North River. Of the 16 cut clams in that data set with sufficient growth for band resolution, 12 were just beginning to deposit their 1982 band at the time of collection (2 August, 3-4 wk earlier than the other sites—Table 2). Two of the 16 lacked the terminal band, whereas the remaining two had already deposited a substantial amount of the 1982 band. This North River local data set was the only one that contained any clams (only three) which had bands sufficiently faint to cause any doubt about recording them.

By counting all presumptive annual bands over the complete growth record of each clam, we also estimated the age of each of the 89 *M. mercenaria* used in this experiment. The estimated age at the experiment's initiation for the 17 clams excluded from our 2-yr tests ranged from 6 to 29 yr and averaged 15.5 yr (±1.7 SE). For the 72 clams that grew sufficiently and included a sufficient shell marker at initiation to be used in our 2-yr tests, age at experimental initiation ranged from 0 to 17 yr and averaged 3.9 yr (±0.3 SE). Thus, the average age of the clams that could not be used for our tests was significantly ($P < 0.01$ in a t-test) higher than that of the 72 clams that were used. Most (16 of 17) of the excluded clams lacked both sufficient growth and an obvious disturbance check at initiation. Only one clam was excluded with sufficient growth but without an adequate disturbance check. Although 16 clams lacked sufficient growth to determine accurately the shell size at the initiation of the experiment and were therefore excluded from our tests, all of these clams possessed discrete bands in their shells that could be counted separately. They were, however, close together at the terminal margin of the shell where separating them was not always possible and caused some uncertainty in their age estimates.

Discussion

Our banding data from recovery of marked and measured *M. mercenaria* after virtually 24 mo of terminal growth provide a compelling case for the reliability across different habitats of using major growth bands in sectioned shells to age hard clams in the Cape Lookout region of North Carolina. Our previous test of the annual periodicity of banding in North Carolina's *M. mercenaria* (Peterson et al. 1983) was carried out in only single locality, a Back Sound seagrass bed, characterized by almost equal proportions by weight of sands and muds in its surface sediments (Table 1). Through this study, we extend our tests of the reliability of annual band deposition in *M. mercenaria* to several additional sites, located in different bodies of water and characterized by much sandier sediments (Table 1). Of the six sites that we used for these tests, three were vegetated by seagrasses and three lacked macrophytic cover (Table 1). (Although our initial experiment in Middle Marsh was situated inside a seagrass bed, seagrasses were removed from the experimental plots during each sampling.) Despite these differences in local geographic location (and probably salinity), sediment grade, and seagrass presence, banding patterns were consistent and bands were deposited annually.

By using relatively high densities of 80 m^{-2} (over 10 times the average natural density found in a Bogue Sound seagrass bed by Peterson 1982, in North River, Bogue, Back, and Core Sounds by Beal 1983, and in Back Sound seagrass beds and sand flats by Peterson et al. 1984), we ran the risk of causing inhibition of growth. In fact, we were unable to analyze growth band deposition in 17 of our 89 clams largely because of insufficient growth in the terminal 2-yr increment. This problem may have been induced by our choice of relatively high density in these experiments, but it does have a natural analog. In areas with relatively slow growth and in older age classes where growth rate slows, aging North Carolina's *M. mercenaria* by counting annual bands in shell cross-section may be more difficult and lead to greater error than the consistency of banding results on our other 72 clams implies (Table 3). Nevertheless, banding even in these generally older clams that were excluded from our analyses was discrete and sufficient to permit us to estimate their ages. Aging does not appear to imply cessation of annual band deposition but only an increased dif-

ficulty in distinguishing one band from another.

Observations on the timing of annual band deposition in this study agree well with our previous results (Peterson et al. 1983). The 6 August-3 September period in 1980 consistently fell within the season of annual band deposition and near the end of the band at all five new study sites. Furthermore, the annual band was still being formed or had just been completed in all clams collected 24 August-3 September 1982. The banding of *M. mercenaria* in North Carolina appears to be a summertime event in contrast to the winter banding in northeastern populations (Barker 1964; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Clark and Lutz 1982).

The only clams that failed to deposit two additional annual bands in the 24 mo of this study were taken from the North River locals. This is also the only group that deviated in the timing of final band deposition relative to the 1982 collection date. Most of these clams had just initiated their 1982 bands at the time of collection in contrast to those from all other sites where 1982 band depositon was either far advanced or even terminated. This difference between sites is probably a consequence of the 3-4 wk earlier date of collection at North River (Table 2). Despite an identical, early collection date, the Back Sound clams transplanted to North River exhibited a pattern of band deposition in 1982 that more closely resembled the other four sites than did the North River local clams. This difference provides our only suggestion of an effect of clam origin, but we have no explanation for the possible effect and do not consider it a serious cause to doubt the consistency of annual band deposition in North Carolina's *M. mercenaria*.

The tests of consistency of annual band deposition across habitats in a local estuarine system provide an additional source of confidence in the accuracy of using internal banding patterns to age *M. mercenaria* in the Cape Lookout region of North Carolina. Concern over the lack of such controlled tests had earlier prompted Clark (1974), Gould (1979), and Jones (1981) to question the widespread assumption of regular periodicity in repeating shell features. Our demonstration of consistency in annual banding across local habitats should remove any doubts about the general applicability of using annual bands to age *M. mercenaria* in the Cape Lookout region of North Carolina. The variation in line deposition patterns which has been shown across habitats for *Protothaca staminea* (Peterson and Ambrose 1985) and among individuals within habitat for *P. staminea* and *Chione fluctifraga* (Hughes and Clausen 1980) does not exist for *M. mercenaria* near Cape Lookout. Our results will not only enable invertebrate fisheries biologists to use growth bands with confidence to age North Carolina's *M. mercenaria* but also should stimulate further research on understanding the environmental causes of variation in bivalve shell deposition patterns.

Acknowledgments

K. Bowers, M. E. Colby, S. R. Fegley, C. Furman, C. Groat, S. A. Hughes, K. C. Pierce, G. W. Safrit, Jr., S. Smith, N. T. Sterman, and J. Tucker provided field and laboratory assistance. V. Page drafted and H. Page photographed Figure 1, adapted from Beal (1983). Reviews by S. R. Fegley, W. Sutherland, and M. C. Watzin improved the paper. This study was sponsored by the Office of Sea Grant, NOAA, U.S. Department of Commerce, under grant No. NA81AA-D-00026, North Carolina Department of Administration.

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CHARLES H. PETERSON
P. BRUCE DUNCAN
HENRY C. SUMMERSON
BRIAN F. BEAL

Institute of Marine Sciences
University of North Carolina at Chapel Hill
Morehead City, NC 28557

STANDING STOCK OF JUVENILE BROWN SHRIMP, *PENAEUS AZTECUS*, IN TEXAS COASTAL PONDS

The increased demand for timely information concerning management of shrimp stocks has renewed interest in developing reliable methods of predicting brown shrimp, *Penaeus aztecus*, crop size for the offshore Gulf of Mexico fishery. Advance information regarding shrimp abundance would also enable elements of the shrimp industry to prepare for a potentially good or poor harvest. Studies exploring the feasibility of predicting the annual abundance of brown shrimp off the Texas coast, initiated in 1960 (Baxter 1963), are based on the premise that postlarval and juvenile shrimp abundances are proportionally related to the subsequent commercial harvest (Berry and Baxter 1969).

A "good" predictor is one that is precise, timely, and cost effective. The abundance of postlarval shrimp as they move from the Gulf of Mexico into coastal bays is determined from semiweekly collections made by the National Marine Fisheries Service, Galveston, at the entrance to Galveston Bay between late February and early May (Baxter 1963). The postlarval shrimp index gives the earliest but least reliable indication of potential harvest. A more accurate but less timely prediction is derived from landings of the bait shrimp fishery. Statistics for bait shrimp landings since 1960 provide the basis for a predictive model developed by K. N. Baxter (Klima et al. 1982) defining the relationship between the bait abundance index and subsequent offshore catch. However, this prediction is not available until mid-June, just prior to the seasonal opening, because recruitment of brown shrimp into the bait fishery does not begin until May (Chin 1960). A third possible indicator is the standing stock size of juvenile shrimp in estuarine nursery areas measured before shrimp emigrate and become vulnerable to the bait fishery. This would provide an estimate earlier in the season than the bait index and may be a more accurate predictor than the postlarval abundance. Predictive capability increases with each successive life stage because of the decreased time span between the estimate and subsequent commercial harvest.

To examine the relationship between juvenile brown shrimp standing stock and offshore harvest, and to determine the suitability of juvenile brown shrimp abundance as a predictor, we conducted a mark-recapture study in Galveston Bay, TX, during the first week of June 1983. In this report we summarize the results of our study, compare estimates

obtained by mark recapture and an alternative drop sampler method, and discuss previously unreported results of 1970-71 studies (Welker and Baxter[1]).

Methods

Sydnor Bayou is a shallow coastal tidal pond in Galveston Bay (Fig. 1). The site was chosen because the single narrow entrance could be blocked easily with netting, thus preventing immigration and emigration of shrimp during the experiment, and because Sydnor Bayou was the site of a similar study in 1970.

The pond covers 32.4 to 36.4 ha, depending on the tide, is about 0.9 km long and 0.2 km at its widest point, narrowing to 6 m at the mouth. Maximum depth is about 1.5 m at high tide, with a 0.25 m tidal difference. Average salinity during the marking was 20.5 ppt and mean surface temperature was 28°C.

Weekly sampling of Sydnor Bayou with a 3 m otter trawl (25 mm stretched mesh) began 25 April 1983 to monitor the size of the juvenile shrimp. By 23 May 1983, most shrimp caught in the trawl were larger than the 40 mm TL (total length) minimum needed for tagging, and we decided to begin the mark-recapture experiment the next week.

Sydnor Bayou was blocked at dawn on 31 May 1983 across bridge B-1 (Fig. 1) with a 45.7 m net having a 6 mm mesh. The net was anchored to the bottom and remained in place for the duration of the experiment.

A 1.8 m diameter, 0.8 m deep round tank with continuous water flow and two 147 L aerated ice chests were set up on shore to hold shrimp during the marking process. Shrimp were caught in 49 5-min trawl hauls and transported to the marking site in aerated 45 L ice chests. To minimize marking mortality, only shrimp 40 mm TL and larger were marked and held in the large tank. Marking was accomplished by injection with pink fluorescent pigment as described by Klima (1965). Representative length-frequency, species-composition, and sex ratio information was obtained from shrimp captured in one trawl haul.

Marked shrimp were released within the hour after the target number (4,100) had been marked. Shrimp were scattered along the shallow grassy shoreline from moving skiffs. No dead or moribund shrimp were released, and release operations ceased whenever shore birds were attracted.

Four 61 cm × 61 cm × 20 cm wire cages, each

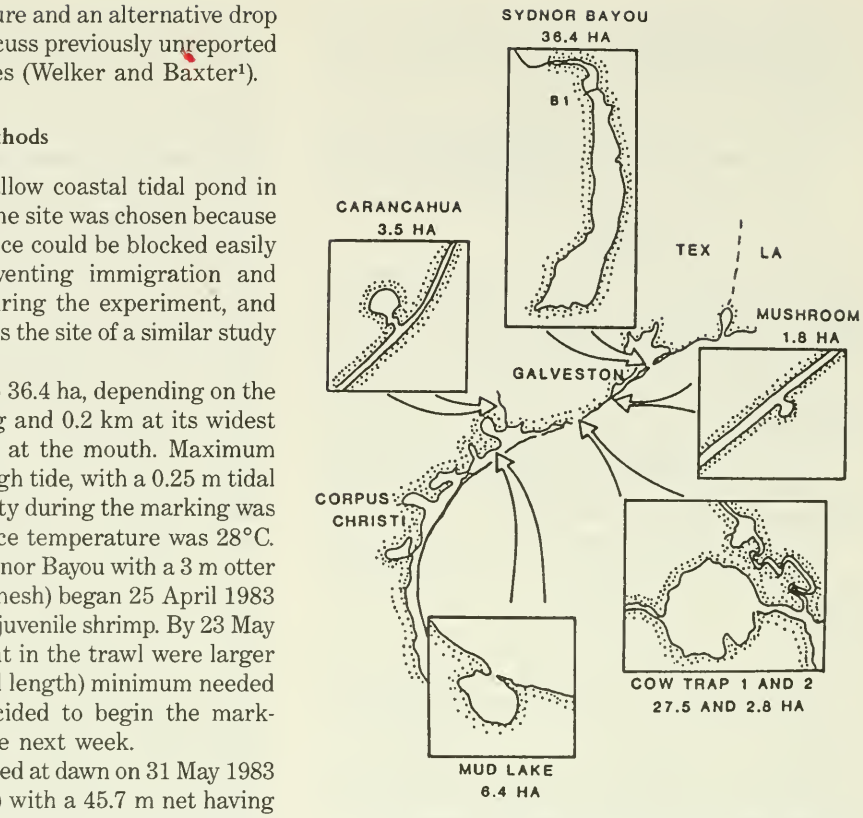

FIGURE 1.—Texas ponds selected for brown shrimp mark-recapture studies: Sydnor Bayou (1970 and 1983); Cowtrap, Mushroom, Carancahua, and Mud Lake (1971).

containing 25 marked and 25 unmarked shrimp, were set out in the pond and remained submerged through all tidal stages. After 24 h, cages were raised and all shrimp, dead and alive, were counted, measured, and recorded for an estimate of marking mortality.

Recapture trawling began 18 h later, allowing marked shrimp time to distribute themselves in the unmarked population. For three consecutive days, all trawlable bottom was sampled by 5-min trawl hauls. Shrimp were returned to the laboratory where marked shrimp were identified under ultraviolet light. All marked and up to 100 unmarked recoveries were measured per tow. Length-frequency distributions for releases, marked recoveries, and unmarked recoveries are shown in Figure 2.

We estimated an initial population of juvenile brown shrimp using Bailey's (1951) modification of the Petersen formula

[1]Welker, W., and K. N. Baxter. Juvenile brown shrimp population estimates in Texas tidal marsh ponds. Unpubl. manuscr., 8 p. Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550.

$$N = M \frac{(C + 1)}{R + 1}$$

where M = number of marked shrimp released, corrected for marking mortality,
C = number of shrimp examined for marks,
R = number of recaptured marked shrimp in the sample.

The 95% confidence limits for the true population were estimated using the standard error of the large sample variance formula (Bailey 1951)

$$V(N) = \frac{M^2 (C + 1)(C - R)}{(R + 1)^2 (R + 2)}.$$

Application of this method is justified under the following conditions (Ricker 1975):

1) Marked shrimp suffer the same natural mortality as unmarked.
2) Marked and unmarked shrimp are equally vulnerable to fishing.
3) Marked shrimp do not lose their mark.
4) Marked shrimp become randomly distributed among unmarked.
5) All marks are recognized and reported on recovery.
6) There is not emigration or immigration occurring in the catchable population.

Results and Discussion

Overall marking mortality was 9%. One cage had unusually high mortality. Nineteen of 25 marked shrimp were alive at the end of 24 h, and the only evidence of the other 6 marked shrimp was pieces of exoskeleton. They apparently molted and were cannibalized. Holt (1982) suggested that the condition of shrimp prior to tagging dictates the survival of the tagged animals. When stressed animals were tagged, mortality more than doubled. Howe and Hoyt (1982) hypothesized that tags and marks may indirectly cause mortality by attracting predators. Farmer and Al-Attar (1979) found shrimp marked with subcutaneous pigment suffered high mortality (compared with controls) only when held with unmarked conspecifics. Clark and Caillouet (1973), however, found negligible marking mortality in a mark-recapture experiment with white shrimp, *P. setiferus*, when 50 marked and 50 unmarked control shrimp were held in a large pen in a pond rather than in several small cages. Costello and Allen (1962) stated that stained shrimp may be expected to survive at essentially the same rate as unmarked shrimp, regardless of presence of predators. To avoid overestimating marking mortality, we did not include the counts in the high cage in the calculation. The resulting 4% (3 dead marked shrimp out of 75) was similar to the marking mortalities of past studies in Sydnor Bayou, Mud Lake, and Mushroom (Welker and Baxter fn. 1).

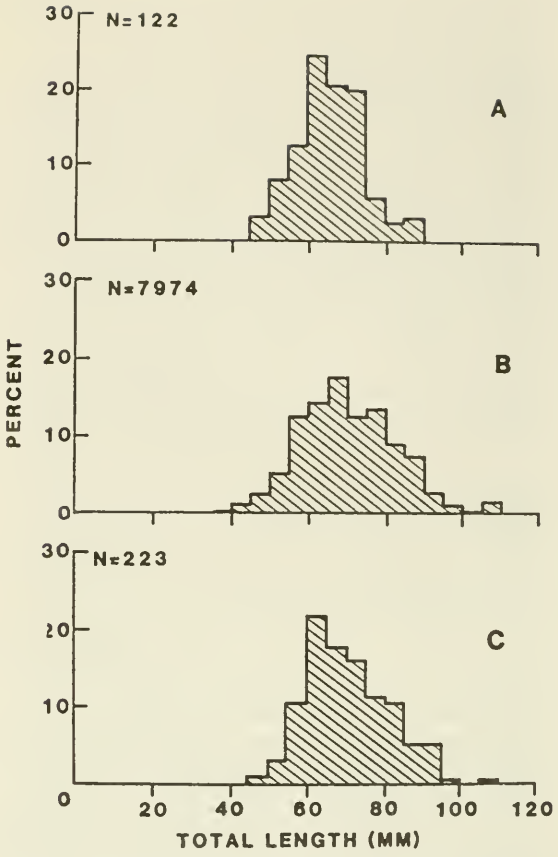

FIGURE 2.—Length-frequency distribution of brown shrimp in Sydnor Bayou, June 1983: A) representative sample of shrimp collected during marking; B) unmarked shrimp caught during recapture operations; and C) marked shrimp caught during recapture operations.

1983 Population Estimate

A total of 223 marked shrimp were among 12,304 shrimp caught in 94 recapture tows. Tides during the recovery period were low in the morning, approaching high tide in the afternoon. Areas along the shore and the south end of the bayou were shallow for trawling in the mornings, but could be adequately sampled in the afternoon. Distribution

of marked shrimp was random (one-sample runs test, $P = 0.960$; Siegel 1956).

The population estimate of 207,786 shrimp determined from mark-recapture data compared favorably with the results of a concurrent drop sampler experiment (Table 1). Shrimp densities were obtained using a 2.8 m^2 drop sampler at high tide. Detailed methodology has been described by Zimmerman et al. (1984). Drop samples were taken in two sets, four pairs each, in vegetated and nonvegetated areas, divided between the south and north ends of the bayou. Vegetated habitat was sampled along the bayou margins, while nonvegetated area sampling was in open waters of the bayou. Numbers of shrimp within the sampler were extrapolated to represent the shrimp population in the vegetated, nonvegetated, and total areas of Sydnor Bayou. Confidence intervals for the drop sampler were much wider than those for Petersen estimate because drop sampler estimates were based on a small number of samples. The drop sampler estimate for 36 ha was higher by about 92,000 shrimp. One reason for this difference is that the mark-recapture estimate reflects only that part of the population >40 mm TL, while the drop sampler measures density of small (<40 mm) shrimp more effectively, and these small shrimp are included in the estimate (Table 2). We calculated the drop sampler population estimate using only shrimp larger than 40 mm TL (Table 1). A chi-square test shows a significant difference between the drop sampler and mark-recapture size-frequency samples, categories 41-50 mm and higher ($\chi^2 = 109.45$, df = 6, P very small). The high chi-square value is due mainly to the greater number of 41-50 mm shrimp and the lower number of larger shrimp (81-90 mm), which may avoid the sampler, in the drop sample. Length-frequency composition of the drop sampler catch indicates that 23% of the 103 shrimp taken were smaller than 40 mm TL, while no shrimp smaller than 40 mm were captured by the otter trawl.

TABLE 1.—Sydnor Bayou brown shrimp population estimates determined by mark-recapture and drop sampler methods, June 1983.

Method	Estimated population	95% C.I.
Mark-recapture[1]		
32.4-36.4 ha	207,786	180,884-234,688
Drop sampler		
32.4 nonvegetated ha	185,000	41,900-479,000
4.0 vegetated ha	115,000	49,000-248,000
36.4 total ha	300,000	90,800-727,000
Drop sampler[1]		
32.4 nonvegetated ha	157,000	113,000-423,000
4.0 vegetated ha	88,000	53,500-183,000
36.4 total ha	245,000	166,000-606,000

[1]Estimate of shrimp population >40 mm TL.

TABLE 2.—Length-frequency composition of Sydnor Bayou brown shrimp samples taken with the otter trawl ($N = 8,197$) and drop sampler ($N = 83$), 1-3 June 1983.

Length (mm)	Otter trawl (%)	Drop sampler (%)
<20	0.0	9.7
21-30	0.0	1.9
31-40	0.0	11.7
41-50	3.8	19.4
51-60	17.3	19.4
61-70	32.2	22.3
71-80	25.7	12.6
81-90	16.0	1.9
91-100	4.2	0.0
>100	0.6	0.8

1970-71 Population Estimates

Our methodology for conducting a Petersen single census mark-recapture experiment with juvenile brown shrimp was developed during June and July 1971 studies of five Texas coastal ponds (Fig. 1). All ponds ranged from 0.3 to 0.9 m in depth during a normal summer tidal cycle. Cow Trap 1 and 2 had considerable emergent vegetation along their shorelines and were part of a large marsh complex. Extensive flooding of the marsh surrounding these ponds at flood tide greatly increased the area accessible to shrimp, but this shallow, vegetated area could not be sampled. Shrimp could move from pond to pond via flooded marsh and ditches, rendering block nets ineffective. Evidence of this movement was the netting of marked shrimp released in Cow Trap 1 and recaptured in Cow Trap 2. These problems precluded reasonable population estimates for the Cow Trap ponds, and large marsh complexes were avoided for future studies of this type.

Mud Lake, Carancahua, and Mushroom had generally well-defined shorelines, even during flood tide, and were not contiguous with other ponds or ditches. Mark-recapture methods were essentially the same as described for the 1983 study. Marking and holding operations were conducted on a portable barge rather than from shore (Emiliani and Marullo 1973). Population estimates determined by Bailey's (1951) formula ranged from 7,490 to 17,119 brown shrimp per hectare (Table 3). The lowest estimate was recorded in Mud Lake, where the highest percentage of total catch was <40 mm TL, while the highest estimate was for Carancahua. The density in Mushroom was close to that in Carancahua.

Although marking methods differed, a 1970 mark-

recapture study in Sydnor Bayou provided a population estimate for comparison. Marking was accomplished by spraying shrimp >40 mm TL with granular fluorescent pigment (Benton and Lightner 1972). Data analysis was as described for the 1983 Sydnor Bayou study. The average density of shrimp in Sydnor Bayou during the 1983 study was 37% of the May 1970 density and was the lowest per hectare estimate of any pond previously sampled (Table 3).

We believe that juvenile brown shrimp population density, determined by the mark-recapture method, may prove to be a good predictor of offshore production as we compile a longer term data base. Although the drop sampler (area-density method) may measure shrimp density more accurately, the Peterson mark-recapture method gives a more precise (having less variance) population estimate.

Acknowledgments

We thank the many people who helped us in the field and processing shrimp; also, Roger Zimmerman, for supplying drop sampler data. We are especially grateful to Don Hanson for allowing us the use of his property along Sydnor Bayou during the study.

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Loretta F. Sullivan

Table 3.—Summary of juvenile brown shrimp population studies in Texas coastal ponds.

Location	Start date	Number 5-min tows	Number shrimp caught	Percent <40 mm	Number marked and released	Percent released and recovered	Percent marking mortality	40+ mm population per hectare	95% confidence interval[1]
Sydnor Bayou									
32.4 ha	5/31/83	49	5,188	0.3	3,994	5.9	4.0	6,412	5,583-7,244
36.4 ha								5,709	4,970-6,448
Sydnor Bayou									
32.4 ha	5/21/70	32	8,045	—	7,718	1.7	4.0	17,933	14,198-20,042
36.4 ha								15,238	12,637-17,839
Mud Lake									
6.4 ha	6/3/71	27	6,750	20.0	6,120	10.8	4.0	7,490	6,956-8,025
Carancahua									
3.5 ha	6/7/71	26	6,301	7.0	4,574	9.8	8.0	15,697	11,815-17,087
Mushroom									
1.8 ha	7/2/71	24	8,348	6.0	4,142	28.8	4.0	14,375	13,628-15,120

[1]Bailey (1951) large sample variance.

Southeast Fisheries Center Galveston Laboratory
National Marine Fisheries Service, NOAA
4700 Avenue U
Galveston, TX 77550
Present address: *178 Plaza Circle*
Danville, CA 94526

Dennis A. Emiliani
K. Neal Baxter

Southeast Fisheries Center Galveston Laboratory
National Marine Fisheries Service, NOAA
4700 Avenue U
Galveston, TX 77550

A POSSIBLE LINK BETWEEN COHO (SILVER) SALMON ENHANCEMENT AND A DECLINE IN CENTRAL CALIFORNIA DUNGENESS CRAB ABUNDANCE

Dungeness crab, *Cancer magister*, are taken commercially along the west coast of the contiguous United States from Avila, CA, to Destruction Island, WA (Fig. 1). During the early years of the California Dungeness crab fishery, effort was concentrated on the central California population which produced most of the state's landings (Fig. 2). The northern population subsequently became the major contributor to California's landings after an expansion of the fishery there during the 1940's.

Northern California landings (Fig. 2) generally have followed a fluctuating pattern similar to one expressed in Oregon and Washington; however, landings from the relatively isolated central California population failed to recover from a coastwide low during the early 1960's. The lower landings reflect a long-term reduction in abundance which has been variously attributed to egg predation by a nemertean worm *Carcinonemertes errens* (Wickham 1979) and to the effects of a long-term change in oceanic conditions (Wild et al. 1983).

The failure of the central California population to recover from the coastwide period of low abundance also occurred about the time coho salmon, *Oncorhynchus kisutch*, reared in Oregon and Washington hatcheries began to make a significant contribution to the west coast salmon fishery (Oregon Department of Fish and Wildlife 1982). The effect of salmonid predation on commercially important marine crustaceans has received little attention, although it is suspected that predation by salmonids introduced into a number of both small and large freshwater lakes (Nilsson 1972; Morgan et al. 1978) has substantially altered the abundance and species composition of their planktonic crustacean communities. Since numerous salmonid food habit studies (Heg and Hyning 1951; Petrovich 1970; Reilly 1983a) show that planktonic Dungeness crab megalops are a major component of the coho salmon diet, it is conceivable that an increase in the coho predation rate associated with an influx of hatchery coho into the central California region is at least partially responsible for the prolonged decline in Dungeness crab landings.

In this paper I first present evidence showing that a large portion of the coho salmon ultimately caught each summer off the west coast are in California waters during spring, the period Dungeness crab megalops are most abundant. I then compare and contrast survival indices to determine if the temporal variation in survival of both species is consistent with the predator-prey hypothesis.

Oregon Production Index Area Coho

Each spring and summer, a single coho salmon brood (year class) is recruited to the commercial salmon fishery off California, Oregon, and southern Washington, an area collectively referred to as the Oregon Production Index area or O.P.I. area (Oregon Department of Fish and Wildlife 1982). These fish entered the ocean to feed in May and June of the previous year, after having spent about 18 months in freshwater. Coho caught in the O.P.I. area before 1961 (Fig. 3) were predominately wild stocks. These stocks had declined to extremely low levels by 1960; however, the successful introduction of Oregon and Washington hatchery-reared coho resulted in a return to historical landing levels during the 1960's and 1970's. Much of the hatchery fish responsible for the increased landings are derived from early return Toutle River coho, which tend to enter fisheries south of their stream of origin (Hopley 1978).

Coho salmon made up only 10% or less of California's ocean salmon catch prior to the development of Oregon and Washington enhancement programs (Fry 1973). Most of these wild coho originated in the streams and rivers of Oregon and Washington (Allen 1965) and were landed primarily in the northern California ports of Crescent City and Eureka. The recruitment of hatchery fish increased the average annual coho contribution to 25% of the total ocean salmon catch, with the central California ports of San Francisco and Fort Bragg accounting for a considerably larger portion of the total coho catch.

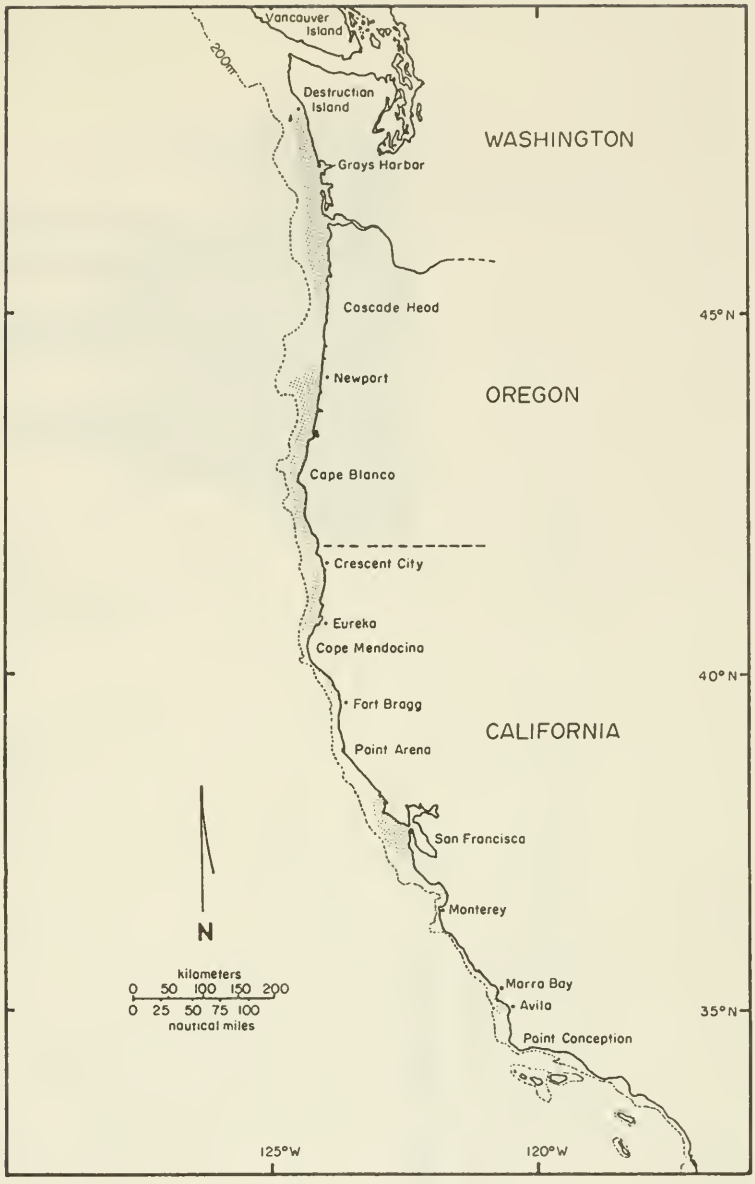

FIGURE 1.—Commercial fishing areas for Dungeness crab off Washington, Oregon, and California. (Pacific Fishery Management Council (1979).)

Before 1973, the California salmon season (coho and chinook) opened on 15 April, although few coho were landed before June because of a minimum size restriction. As Oregon and Washington hatchery coho became available, a substantial increase in the hook and release of sublegal ("shaker") fish developed during the latter half of April to the middle of June. In an attempt to reduce the shaker problem, the season opening for coho was delayed until 15 May and the minimum size was reduced in 1973 (O'Brien and Lesh 1975).

California coho catches generally peak in July, then drop sharply in August, 2 mo before the salmon season closure. The midsummer decline is attributed to the northward exodus of fish returning to their natal stream to spawn (Fry 1973). It is however unclear when and by what route these fish entered California waters.

A general migration model (Loeffel and Forster 1970; Godfrey et al. 1975; Hartt 1980) proposes that newly emigrated west coast coho move immediately northward into the Gulf of Alaska, then during winter, undertake a southeasterly migration which brings them back into California, Oregon, and Wash-

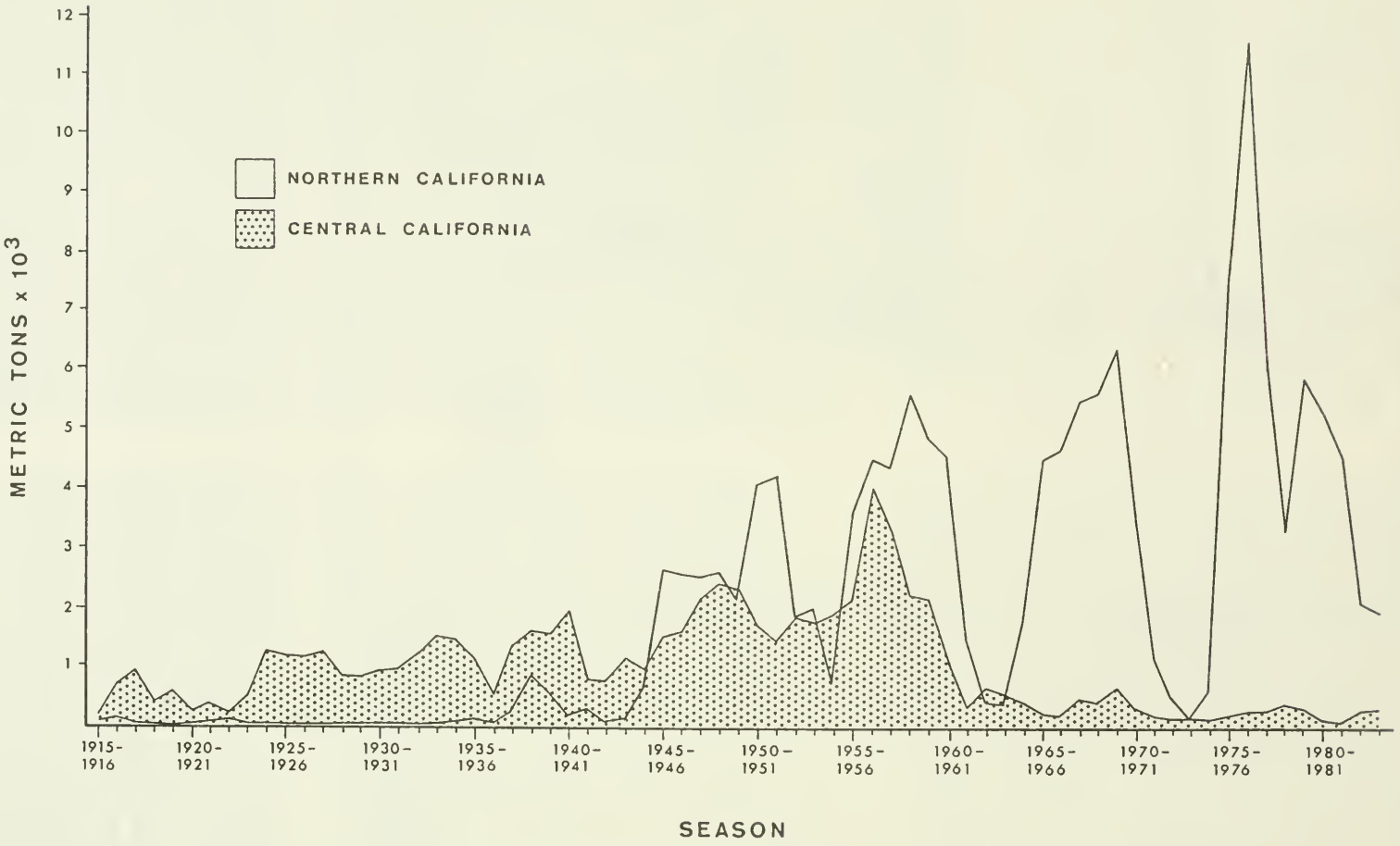

FIGURE 2.—Northern California (Crescent City, Eureka, Fort Bragg) and central California (Bodega Bay, San Francisco, and Halfmoon Bay) commercial Dungeness crab landings in thousands of metric tons, 1950-51 through 1983-84 seasons.

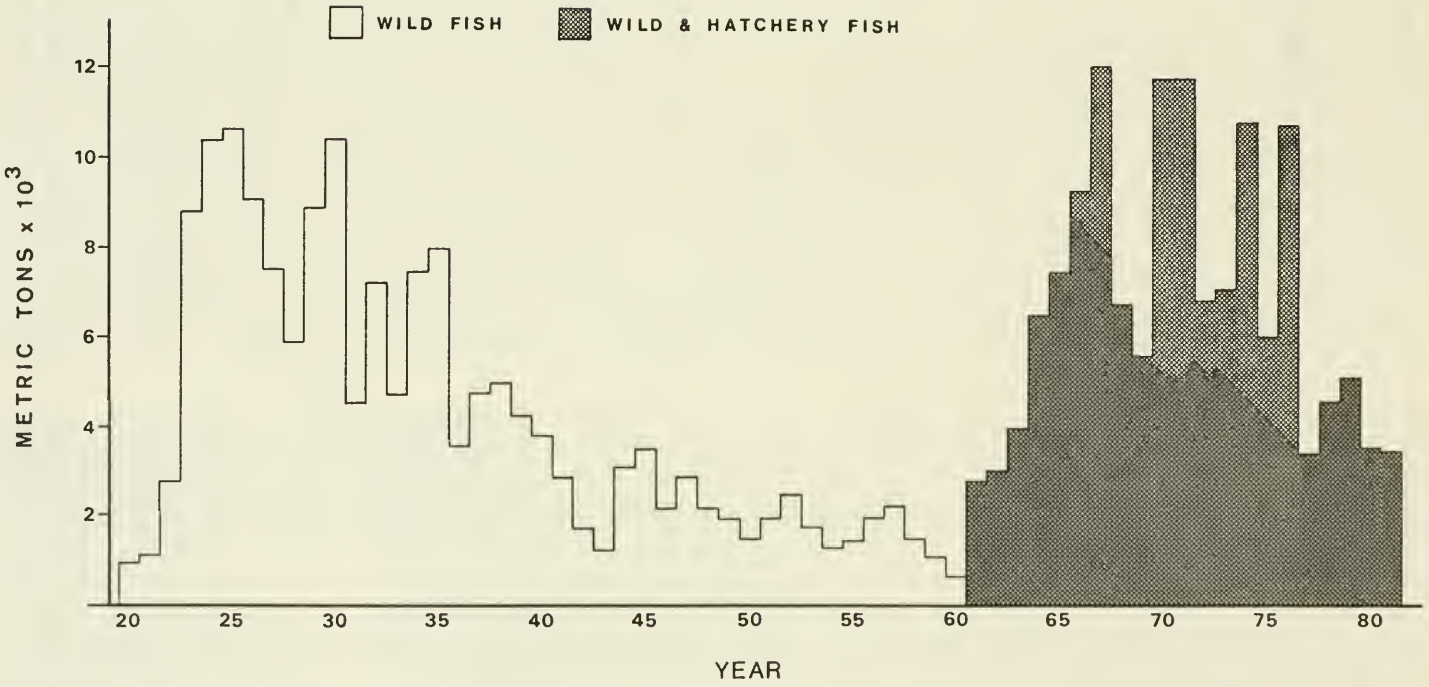

FIGURE 3.—Coho salmon landings in the Oregon Production Index area, 1920 through 1981, in thousands of metric tons. Figure adapted from Oregon Department of Fish and Wildlife (1982).

ington coastal waters each spring. Coho returning to the coast south of their natal stream would subsequently undergo the observed northward spawning migration. Each of these authors conceded however, that certain stocks or different portions of the same stocks may follow entirely different migratory routes. Scarnecchia (1981) felt that many coho produced along the west coast may either remain in adjacent coastal waters or move directly south after emigration from freshwater.

The dispersal pattern of 437 coho salmon tagged off northern California early in the 1971 and 1972 seasons clearly showed the northward movement of adult coho out of California (O'Brien 1973). Nearly all of the tagged fish recaptured in California were caught in May and June of each year while tagging was still being conducted. Oregon recoveries peaked in July and the first half of August, while most Washington recoveries occurred during the latter half of August through September.

California's share of the recaptured coho tagged off northern California (O'Brien 1973) was 9.3% in 1971 and 8.8% in 1972. These percent returns are very similiar to California's 13.0% and 8.3% share of the O.P.I. area catch in 1971 and 1972 respectively. Because, for practical purposes, one can assume that all of the coho caught in California originate to the north, the similarity between California's catch and tag returns would indicate that nearly all O.P.I. area coho stocks were off California during the tagging period. This supposition is extreme, but the results do suggest that a major portion of the coho ultimately caught in the O.P.I. area each year are in California waters during spring. The northward migration of large numbers of coho is further supported by the northward progression of peak monthly catches within the O.P.I. area (Pacific Fishery Management Council 1983), and the monthly catch distribution of hatchery marked coho (Hopley 1978).

Survival Indices Comparison and Discussion

Dungeness crab, unlike coho salmon, do not move any appreciable distance, therefore local landings are considered to be a good indicator of local abundance. In California seasonal landings are composed of at least three year classes, however northern California landings are generally dominated by 4-yr-old crab (Warner 1985), while central California landings, because of a faster growth rate, are dominated by 3-yr-old crab (Collier[1]).

An alignment of Dungeness crab seasonal landings with their dominant or "primary" year classes (Fig. 4) generates reasonably representive year class indices, if it is taken into consideration that extremely abundant year classes, such as the 1966 and 1972 year classes in northern California, probably dominate landings for more than 1 yr (Methot and Botsford 1982). The Dungeness crab year class indices (Fig. 4) suggest that a period of poor landings in both central and northern California during the early 1960's (Fig. 2) reflects poor survival of the 1958-60 year classes.

As mentioned earlier, northern California landings have been characterized by large seemingly cyclic fluctuations, the cause of which has been the subject of considerable research and debate (see Methot and Botsford 1982; Botsford 1984, for a review of this work). Of the hypotheses generated by these investigations, Wild et al. (1983) presented, in my opinion, the most tenable explanation for this particular period of low survival. They attributed the drop during this period to a reproductive failure caused by an unprecedented warming of coastal waters associated with the 1957 El Niño (the "warm water years" 1957-59, Radovich 1961).

The apparent recruitment of Dungeness crab to the northern California population of a "normal" year class in 1961 (Fig. 4), with the return of "normal" environmental conditions, ushered in several years of good survival. This recovery was not duplicated in the central California population, where a drop in the strength of the 1961 year class anteceded an extended period of poor survival. Wild et al. (1983) further proposed that a major change in the oceanic regime off central California is the primary cause of the continued poor survival there, although they do concede that ocean temperatures in certain years appear to have been favorable to Dungeness crab survival. Wickham (1979), on the other hand, suggested that the central California population has reached a new equilibrium, with worm predation now being the dominant biological control. It has yet to be proven which, if either, of these mechanisms is the primary cause of the continued poor survival in central California.

Alternatively, a direct comparison of O.P.I. catches with central California Dungeness crab year class indices (Fig. 5) illustrates a long-term inverse relationship which developed with the first recruitment of hatchery-reared coho salmon stocks in 1961. O.P.I. area landings are used to express the annual survival of coho potentially impacting central Califor-

[1]P. Collier, California Department of Fish and Game, 619 Second St., Eureka, CA, 95501, pers. commun. November 1984.

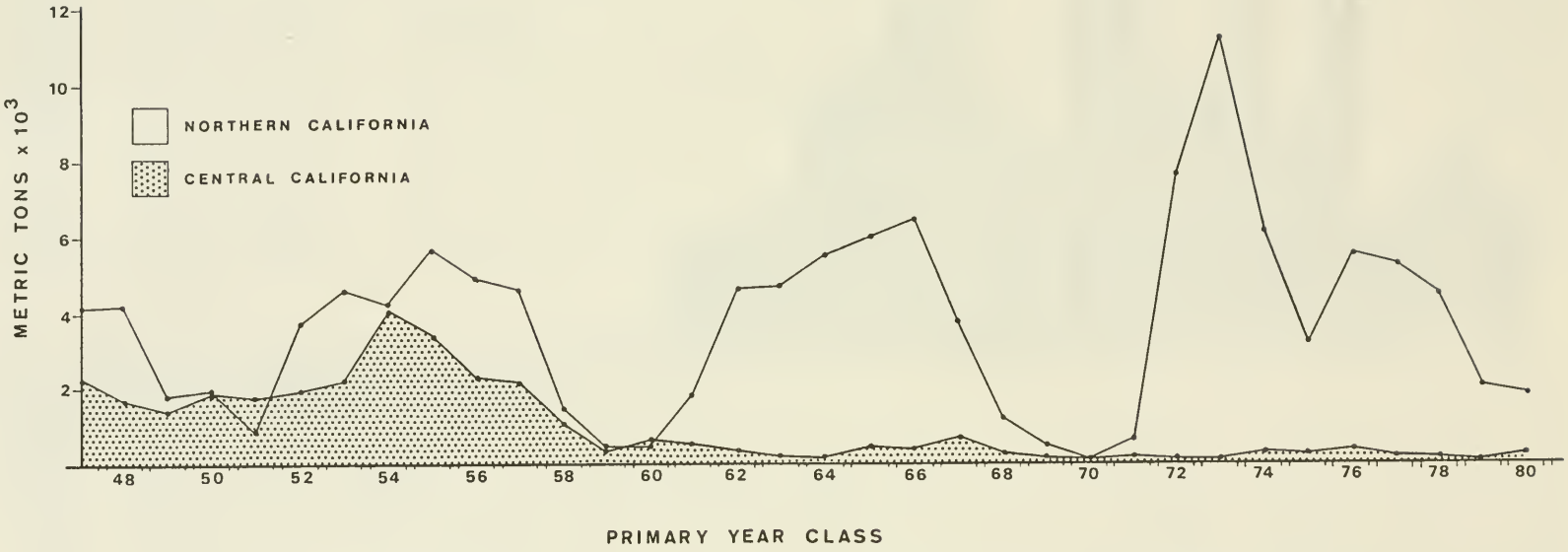

FIGURE 4.—Alignment of "primary" Dungeness crab year classes (1947-80) with the seasonal landings they dominate. Landings are lagged 3 yr in central California and 4 yr in northern California.

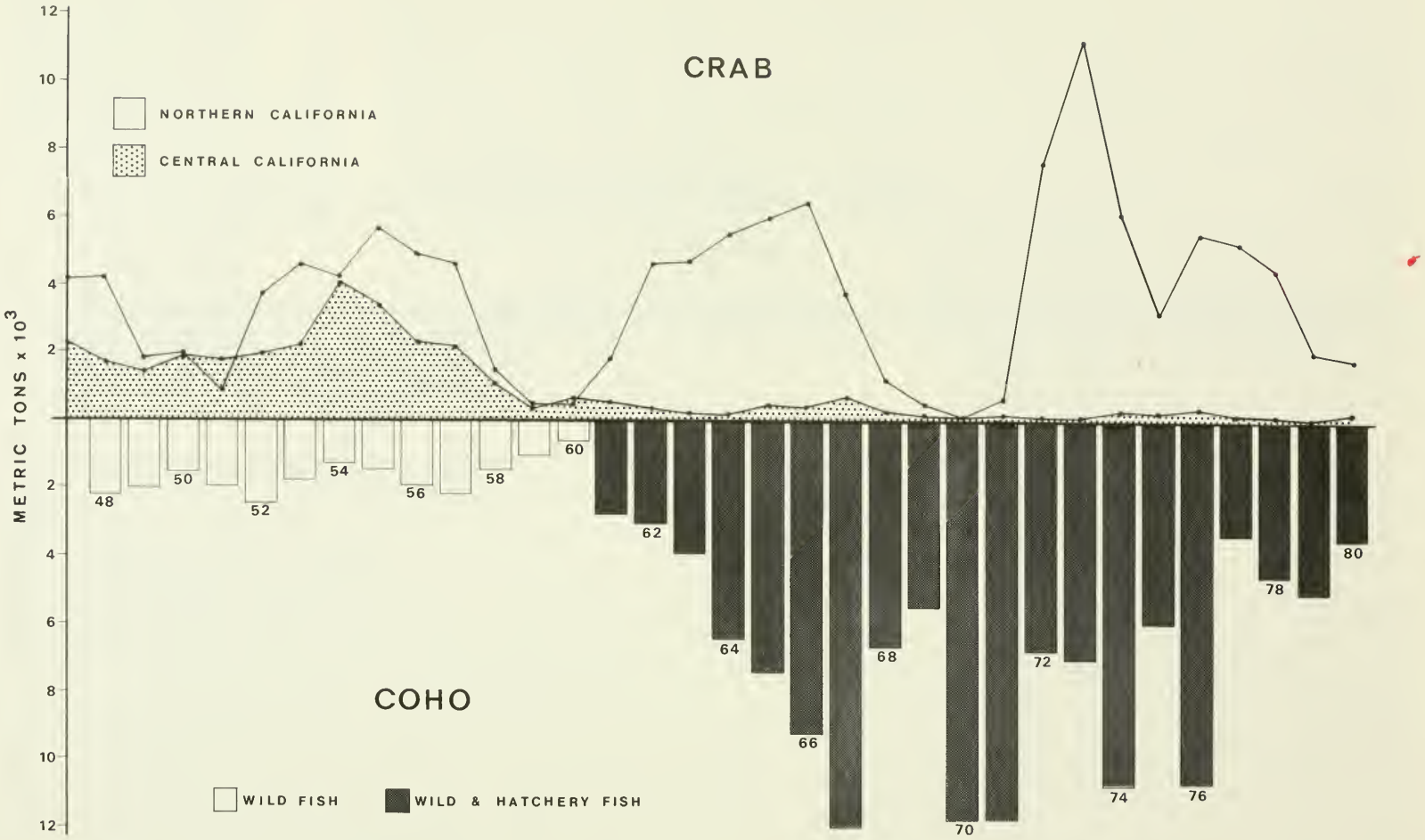

FIGURE 5.—Northern and central California Dungeness crab year class indices (primary year classes) 1947-77, aligned with Oregon Production Index area coho salmon landings, 1948-80.

nia Dungeness crab because of the evidence that California catch statistics underestimate the number of fish actually in the state during spring. These landings provide a straightforward measure of brood survival that is independent of distribution and local catchability.

Even though the relatively low O.P.I. area landings in 1961, 1962, 1963, 1977, and 1980 are comparable with the predecline era, the general pattern of correspondence in Figure 5 is consistent with an increase in the coho salmon predation rate on Dungeness crab megalops. Within the framework of the predator-prey hypothesis, the association of low O.P.I. area coho catches during the early years of the hatchery era with reduced Dungeness crab survival would indicate that a relatively small number of hatchery coho can effectively surpress megalops survival. This is particularly apparent when it is considered that hatchery production was at a minimum during the 1961-63 period and wild fish still dominated the catch (Oregon Department of Fish and Wildlife 1982).

The proposed impact of hatchery coho salmon on the Dungeness crab resource is best explained by the differences in the "functional response"[2] of wild and hatchery coho salmon. In controlled behaviorial experiments, Glova (1978) found that hatchery fry (43-88 mm) were largely nonterritorial, exhibiting a stronger tendency to aggregate than the wild fry. This behavioral pattern is believed to be the direct result of the unnaturally high densities found in hatchery operations. If adult hatchery coho retain this behavior, the tendency for Dungeness crab megalops to aggregate or "swarm" in coastal surface waters (Lough 1976) would theoretically make them more susceptible to predation (Eggers 1976). Also a reduction in the number of "search images" available to hatchery fish is believed to result in a more homogenous diet (Sosiak et al. 1979). Under these circumstances Dungeness crab megalops may become a more important component of the hatchery coho salmon diet.

The apparent good survival of the 1961-66 year classes in northern California (Fig. 5) suggests that the majority of the hatchery coho salmon produced during those years concentrated to the south of that population during the period when Dungeness crab megalops are most abundant. This supposition, together with recently acquired evidence that the central California Dungeness crab population is at least partially dependent on the recruitment of southward drifting megalops (Hatfield 1983; Reilly 1983b), further suggest that the theoretical predation zone critical to the central California population lies somewhere in the region of strong upwelling and high productivity between the two populations (Fig. 1). Not surprisingly, commercial fishermen have found coho salmon concentrated either before or early in the season in this region. The coho salmon stocks initally released during the early 1960's may possess an inate affinity for these waters.

Northern California landings of the Dungeness crab declined again during the 1970-71 season (Fig. 2). This period of low landings is apparently due to poor survival of the 1967-71 year classes (Fig. 5), which cannot be readily explained by an extended period of warmer than normal water. The various hypotheses to explain the northern California fluctuations notwithstanding, it is possible that hatchery-reared coho salmon began to limit Dungeness crab survival in northern as well as central California, concomitant with increased hatchery production[3] and/or environmental caused changes in distribution. There is some evidence from coho tagging that supports this supposition.

O'Brien (1973) reported that 17.3% of his returned tags were found in Oregon and Washington hatcheries during the 1971 season, whereas in 1972 only 3% were found in the hatcheries. An exceedingly strong 1972 Dungeness crab year class in northern California (Warner 1984) is in direct contrast with the very weak 1971 year class (Fig. 5) and is inversely related to the small number of tags found in hatcheries during the 1972 season. The small percentage of hatchery returns in 1972 suggest that there were fewer hatchery coho available for tagging in the northern California area during the 1972 season, and this could indicate relatively poor survival of hatchery fish throughout the O.P.I. area. It should be remembered that hatchery-reared coho theoretically have a much larger effect on Dungeness crab survival than wild fish.

Between 1972 and 1977 (Fig. 5), O.P.I. area coho survival and northern California Dungeness crab survival became more erratic. The association of relatively good Dungeness crab survival with good coho landings in 1974 and 1976 may, however, only indicate that coho were farther south than usual. McLain and Thomas (1983) showed that both 1973

[2]In predator-prey theory "functional response" is defined as the relationship between the rate at which individual predators consume prey and the density of that prey (Holling 1959).

[3]The number of hatchery-reared coho salmon released in the O.P.I. area increased from 7.5 million fish in 1960 to 60.8 million fish in 1981 (Oregon Department of Fish and Wildlife 1982).

and 1975 were years with an unusually weak California Countercurrent, or conversely, stronger than normal southward flow and cooler than normal coastal waters. If yearling coho do move directly into California waters after emigration from freshwater, then these anomalous conditions may have caused these fish to move farther south than usual, with the result that adult coho would have been south of the predation zone critical to the northern California Dungeness crab population in the spring of 1974 and 1976.

Since 1976 O.P.I. area coho landings have undergone an inexplicable decline in spite of increasing hatchery production. Theoretically, an increase in Dungeness crab survival should have accompanied this drop in coho survival. The drop in Dungeness crab survival, evident in Figure 5, is obviously inconsistent with the general theory but can be explained in two ways. First, it should be considered that the earlier O.P.I. area coho landings contained far fewer hatchery fish than those during the later years. It has been estimated that hatchery fish comprised 75% of the west coast coho catch by 1977 (Scarnecchia and Wagner 1980). Secondly, a coastal warming trend that began in 1976 (McLain 1983) may have resulted in a northward shift in coho distribution with a concomitant reduction in Dungeness crab megalops survival.

If coho have become the major limiter of Dungeness crab megalops survival within California, then the observed survival patterns suggest that a group of coho, possibly representing the original hatchery stocks, still experience consistently good survival and continue to move into the predation zone critical to the central California population. On the other hand, the more irregular Dungeness crab survival observed in northern California suggest that megalops survival there is more dependent on the vagaries of hatchery-reared coho distribution associated with environmental nuances.

Admittedly, most of the evidence used to support the predator-prey hypothesis is circumstantial. Nevertheless, three of the considerations presented —1) the fact that coho feed heavily on Dungeness crab megalops, 2) the evidence showing that many, if not most, Oregon and Washington hatchery coho are in California during the period megalops are most abundant, and 3) the coincidence of the extended central California Dungeness crab decline with a large increase in the number of hatchery coho within the O.P.I. area—suggest a possible relationship that deserves attention.

The capricious nature of predation on the early life stages of commercially important invertebrates undoubtedly contributes to the difficulties encountered when attempting to manage these relatively short-lived species on a sustained yield basis. If the hypothesized relationship between coho salmon and Dungeness crab eventually proves to be correct, then the salmonid enhancement process itself can be considered an experiment, offering insight into the role predators play in controlling the commercial abundance of many marine species.

Acknowledgments

I would like to thank Bob Tasto, John Geibel, Ron Warner, and two anonymous reviewers for reviewing the manuscript. Special thanks are also due Bob Tasto, who offered considerable encouragement, and Anita Thomas for drafting the figures.

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DAVID H. THOMAS

Marine Resources Region
California Department of Fish and Game
411 Burgess Drive
Menlo Park, CA 94025

THE EFFECTS OF NET ENTANGLEMENT ON THE DRAG AND POWER OUTPUT OF A CALIFORNIA SEA LION, *ZALOPHUS CALIFORNIANUS*

Interactions between pinnipeds and fisheries can be broadly divided into two categories: the role of pinnipeds on the mortality of commercially important fish species and the effect of commercial fisheries on the dynamics of pinniped populations. Although the former has received considerable attention (Hirose 1977; Fiscus 1979, 1980; Matkin and Fay 1980; DeMaster et al. 1982), the importance of the latter has been addressed only recently (Shaughnessy 1980; Fowler 1982; Scordino and Fisher 1983[1]).

Fishery interactions may affect pinniped stocks through changes in prey abundance, incidental takes, or entanglement in discarded fishing gear and plastic packing bands. Scordino and Fisher (fn. 1) have shown that the number of entangled northern fur seals, *Callorhinus ursinus*, on the Pribilof Islands, AK, has recently increased, and now comprises 0.4% of the harvested animals. Fowler (1982[2]) reviewed existing data concerning the accumulation of plastic litter on beaches of several Alaskan islands. Using the number of net fragments found on shore as a rough estimate of the size distribution of material adrift at sea, he concluded that at least 60% are larger than those measured on fur seals. Because most nets found on these animals weigh <600 g, a significant mortality undoubtedly occurs at sea from entanglement in larger fragments.

This paper evaluates the hydrodynamic effect of net entanglement and documents the behavior of an entangled animal. A California sea lion was trained to allow itself to become entangled in a twine trawl net fragment and the subsequent rise in drag was measured. Increased energy consumption and swimming power requirements associated with dragging net fragments were calculated from these measurements. The results provide an initial basis for assess-

[1]Scordino, J., and R. Fisher. 1983. Investigations on fur seal entanglement in net fragments, plastic bands and other debris in 1981 and 1982, St. Paul Island, Alaska. Background paper submitted to the 26th Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 33 p.

[2]Fowler, C. W. 1982. Entanglement as an explanation for the decline in Northern fur seals of the Pribilof Islands. Background paper submitted to the 25th Annual Meeting of the Standing Scientific Committee, North Pacific Fur Seal Commission, 24 p.

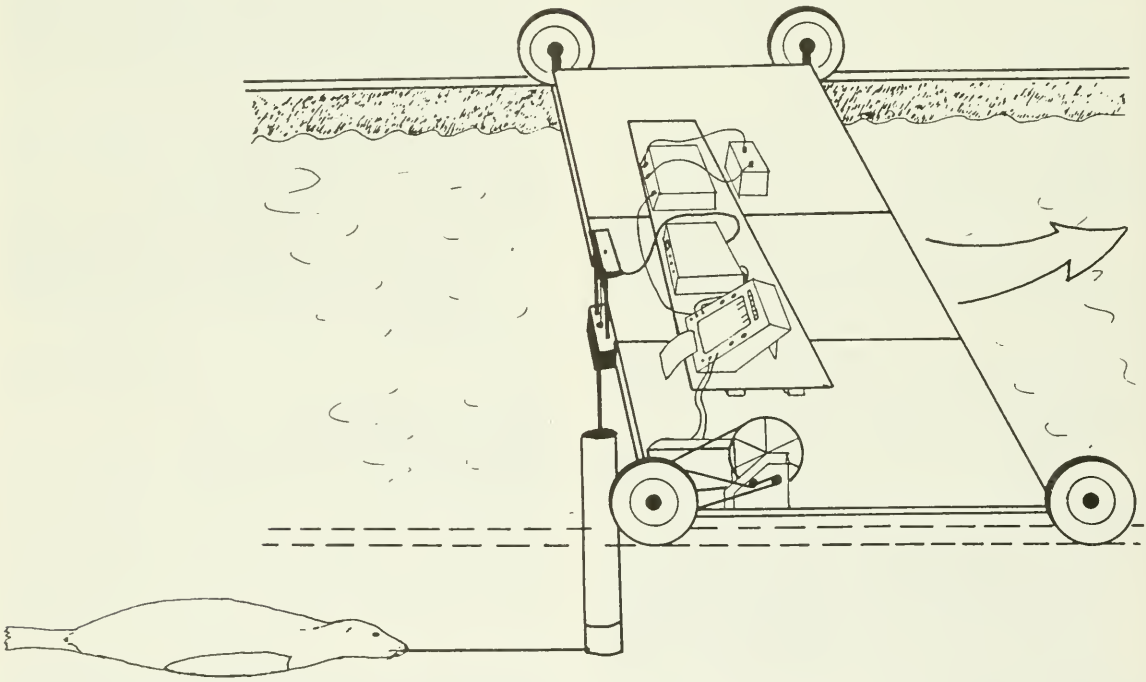

FIGURE 1.—Instruments and cart used in the drag experiments. The sea lion was towed passively underwater and the resultant force recorded. See text for further details.

ing the possible role of net entanglement on the mortality of pinnipeds at sea.

Materials and Methods

A female California sea lion, *Zalophus californianus*, was used in this work. The animal was kept in large seawater holding tanks at Scripps Institution of Oceanography. Its weight (45 ± 0.5 kg) remained constant throughout the course of this study, conducted during April 1983.

To measure drag, the sea lion was trained to bite onto a neoprene mouthpiece and be towed through the water behind a moving cart (Fig. 1). The cart, powered by a variable speed electric motor, travelled around a circular "ring" tank which had a depth of 3.5 m and inner and outer diameters of 14.5 and 21 m, respectively. A line was connected to the mouthpiece and the other end secured to a load cell (Western Scale Co.) which produced a voltage output proportional to the amount of tension on the line. The tow line extended down from the load cell, through a streamlined strut and around a teflon pulley attached to the end of the strut (Fig. 1). The pulley, enclosed by a streamlined fiberglass housing, was set at a depth of 1 m (>3 body diameters) to eliminate surface wave effects on drag (Hoerner 1959).

Drag was measured by continuously recording the signal output from the load cell during each towing session. The signal was amplified and recorded on a Brush[3] 220 strip chart recorder (Gould Instruments). At the end of each session, the load cell was calibrated using a hand-held dynamometer. A tachometer, attached to one of the outer cart wheels, was used to determine cart velocity. This was simultaneously recorded on the strip chart. The sea lion's velocity, while it was being towed down the middle of the tank, was computed using the speed of the outer wheel and the tank's circumference. After each experiment the data were smoothed by eye and drag and velocity determined. Only steady traces which varied less than ±3% were analyzed. Drag was then converted to newtons by multiplying the kilogram force reading of the load cell by the acceleration of gravity.

Once the sea lion's drag without a net was measured, the animal was trained to place its head through an opening cut in the mesh of a 1/8-in (3.2 mm) nylon twine trawl net. The opening was near the center of the net which measured 1.4 m × 5 m, with a stretched mesh size of 19 cm. The net had a dry weight of 580 g. After several trials, the sea lion became accustomed to the procedure and would allow itself to be towed with the net trailing from its neck. The net was removed after each session.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Drag on the sea lion, both with and without the net, increased with velocity (Fig. 2). This rise, however, was significantly greater when the animal was entangled, with the difference between the two curves increasing throughout the range of speeds. At the highest velocity of 3.5 m/s, the entangled drag was 111 N greater than that of the free animal (Table 1). Therefore, to maintain a cruising speed of 2.0 m/s an animal of this size, entangled in a net with similar hydrodynamic characteristics, would experience the equivalent drag of a free animal swimming at speeds above 4 m/s.

Power that the sea lion must expend for swimming can also be calculated from these measurements. Since drag is a force, power output (in watts) is a product of drag times swimming velocity (Webb 1975): P_0 = drag × velocity. Table 1 shows the results of such calculations and the effect of the net on the sea lion's required output.

Power output is a measure of the mean rate of energy expended by the swimming muscles at a given velocity (Webb 1975). It does not, however, reveal the total energetic requirements of the sea

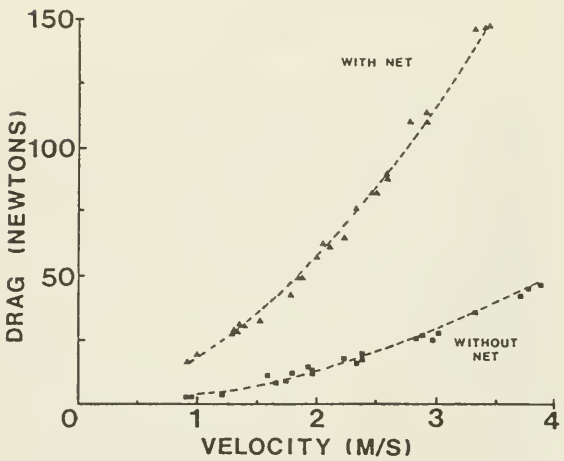

FIGURE 2.—Drag of a 45 kg sea lion with and withoug a net trailing from its neck. In both cases drag increased geometrically with speed. The regression equation with the net was $17.19\ \text{vel.}^{1.73}$, SEE (standard error of estimate) = 0.052. The equation for drag without the net was $2.93\ \text{vel.}^{2.06}$, SEE = 0.118.

TABLE 1.—The increase in drag and power output, and the estimated power input of the entangled sea lion. Drag with and without the net was calculated from the best fit regressions determined by the experiments. Power output was calculated by multiplying drag and the appropriate velocity. Weight specific power input is based on an efficiency (power out/power in) of 10%.

	Velocity (m/s)					
	1.0	1.5	2.0	2.5	3.0	.3.5
Drag (N)						
Without net	2.93	6.75	12.21	19.33	28.13	38.64
With net	17.19	34.66	57.01	83.87	114.97	150.11
Power output (W)						
Without net	2.93	10.13	24.42	38.65	84.40	135.24
With net	17.19	51.99	114.02	167.74	344.91	525.39
Power input (W/kg)						
Without net	0.7	2.3	5.4	8.6	18.8	30.0
With net	3.8	11.6	25.3	37.3	76.6	116.8

lion. Animals are not 100% efficient in converting metabolic energy to mechanical power needed for locomotion (Tucker 1975). Studies of penguins and fish which swim with their pectoral fins show that efficiency (power output/power input) varies between 5 and 15% (Webb 1973; Hui 1983). Female northern fur seals consume about 8 W/kg while at sea (Costa and Gentry in press). Using this number, the power output values estimated for the sea lion, and an assumed cruising speed of 2.5 m/s, an efficiency for fur seals of roughly 10% is obtained. Table 1 shows estimated energy requirements based on this efficiency for the sea lion with and without the net. Again it can be seen that to maintain a swimming speed of 2.5 m/s the sea lion would need to increase its metabolic expenditure by 50-fold, an impossibly high figure (Bartholomew 1977).

Discussion

There is little doubt that for an animal of this size, entanglement in a 600 g net will substantially increase its chance of mortality at sea. Drag, and hence the power required for swimming, is increased by the presence of a net. As a result, these animals will swim slower, at a greater energetic cost than free animals. Drag of the net, which rises geometrically with velocity, will prevent activities requiring high speeds as would be the case if such animals engaged in the pursuit of rapidly moving or evasive prey species. Additionally, migration or travel to and from the rookery will be energetically more costly. It is likely, then, that once an animal becomes entangled in net fragments of this size or larger, it enters a state of negative energy balance.

The animal's size as well as the size of the net plays an important role in the amount of drag experienced. A larger net will present more surface area to the water. Since drag is dependent on surface area (Vogel 1981), larger net fragments will result in greater drag. Similarly, if two different-sized animals are entangled in nets of the same dimensions, the smaller will experience a larger relative increase in its drag and power requirements. If animals of different age classes encounter net fragments with equal probability, it is expected that the younger age classes will suffer a proportionally higher mortality.

Although starvation is undoubtedly the long-term result of net entanglement, other factors may have a more immediate effect. This was particularly evident during an observation of an actual entanglement. In the initial training phase of the sea lion, a net with a larger mesh size was used. At one point, while the net was floating in the water, the sea lion swam up from below and inserted its head through one of the mesh openings. Upon sensing the net around its neck it gave a strong backwards stroke, trying to retract its head. The backward movement brought some of the trailing net in front of it and when the animal then swam forward and dived underwater, another strand slipped onto its neck. This caused a violent reaction with the sea lion twisting and thrashing wildly. The twisting further entangled the animal and tightened the net. Within 1½ to 2 min the animal was completely entangled with three or four loops of mesh tight around its neck.

The net was so tight that an observer on the side of the tank was unable to pull it from the sea lion's head, and it was necessary to drain the holding tank. During this time, the animal swam around the tank barking and often thrashing about while trying to bite the net. This appeared to further tighten the net which, when finally removed, was so tight that a finger could not be slipped between the net and the animal's neck.

If the behavior of otariids at sea is similar to that exhibited by the entangled sea lion, then drowning may be another more immediate cause of mortality. Twisting and rolling could foul the foreflippers and prevent the animal from swimming. This seems particularly likely if it became caught in a larger net. Additionally, because the net was so tightly wrapped around the sea lion's neck, necrosis of the skin tissue and an open wound may have occurred within a matter of hours to a few days. Constant swimming could continue to tighten the net. Although several authors (Scordino and Fisher fn. 1) have speculated that neck wounds indicate a period of entanglement longer than 4 mo, these observations suggest that beached animals with open wounds may have become tangled only a few days prior to sighting.

Acknowledgments

The sea lion was made available for this research by L. H. Cornell, Sea World of San Diego. The assistance provided by Phil Thorson and Terrie Williams in feeding and training the sea lion is gratefully acknowledged and appreciated. C. Fowler, J. Graham, G. Kooyman, and T. Williams provided useful comments on the manuscript.

This study was supported by NOAA grant 82ABC-02743 from the National Marine Mammal Laboratory to G. L. Kooyman.

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Steven D. Feldkamp

Scripps Institution of Oceanography
Physiological Research Laboratory A-004
La Jolla, CA 92093
Present address: *Long Marine Laboratory*
University of California at Santa Cruz
Santa Cruz, CA 95064

NOTES ON THE LIFE HISTORY OF THE CATSHARK, *SCYLIORHINUS MEADI*

The catshark, *Scyliorhinus meadi* (family Scyliorhinidae) is a rare, poorly known species, easily identified by the eight dark saddle-like blotches along the dorsal surface. Springer (1966) first described *S. meadi* and Springer and Sadowski (1970) assigned it to subspecies status of *S. retifer*. In Springer's (1979) revision of the family, it was again given species status. At present only 10 immature specimens of *S. meadi* have been collected, seven males (180-490 mm in length), two females (235 and 385 mm in length), and one 190 mm specimen of unknown sex. This paper reports on the collection of an additional specimen of *S. meadi* and provides valuable life history information.

During a cruise aboard the RV *Delaware II* on 5

May 1984, a specimen of *S. meadi* was collected at a depth of 412 m using a 17 m otter trawl at lat. 28°59.85'N, long. 79°55.98'W. The shark measured 430 mm in length and weighed 0.4 kg. This shark, together with its stomach contents, is deposited at the Ichthyological Museum of the Florida Department of Natural Resources, St. Petersburg (FSBC 16208). Examination of the reproductive system revealed a developing right ovary measuring 4.4 cm long and 0.6 cm wide. The left ovary was atrophied. Follicles teased from the right ovary measured 0.75 mm in diameter. The nidamental glands were 3.0 mm wide and 8.0 mm long. The oviduct, from nidamental gland to vagina, was 82 mm long and 1.0 mm wide. Gut content examination revealed several cephalopod beaks and tentacles, shrimp remains, and the articulated caudal skeleton from a relatively large, unidentified teleost.

This specimen of *S. meadi* is the third and largest female collected to date. Burgess et al. (1979) reported on the collection of a 385 mm total length female in which the right ovary measured 33.2 mm and the left 8.9 mm in length. This represents about 8.6% of the total length of the shark. The right ovary of the specimen reported in this paper represents about 10.2% of the shark's total length. This specimen is immature, but the allometric increase in ovary length, and the fact that the left ovary was completely atrophied suggests that the specimen might be considered a subadult (maturation begun). The small size of the Florida Bahama specimens compared with the North Carolina examples led Burgess et al. (1979) to suggest geographical size segregation. This large specimen from off the central Florida east coast does not support this segregation. Discovery, in gut content examination, of the large, teleost caudal skeleton suggests an unexpected ability to prey on relatively large fishes.

Acknowledgments

I would like to thank David Camp, Mark Leiby, Bill Lyons, Mike Murphy, Jim Quinn, Steve Ealsh, and the captain and crew of the RV *Delaware II*.

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Glenn R. Parsons

Department of Marine Sciences
University of South Florida
140 Seventh Avenue South
St. Petersburg, FL 33701

A COMPARISON OF SCALE AND OTOLITH AGING METHODS FOR THE ALEWIFE, *ALOSA PSEUDOHARENGUS* [1]

Beginning in 1971, the Maine Department of Marine Resources monitored the harvests of anadromous alewives ascending the Damariscotta River (Libby 1982). Part of this monitoring assessed changes in age composition within and between years. Aging was done by interpreting the number of scale annuli in terms of fish age as has been done in earlier investigations (Havey 1961; Rothschild 1963; Marcy 1969). However, scale annuli were sometimes difficult to interpret, so in 1979, methods for removing and reading alewife otoliths were studied. A relatively fast and efficient method was developed for removing otoliths. The ease with which the otoliths were processed to age fish prompted an analysis of which method (scales or otoliths) was best for determining the age of an alewife. This paper compares the precision of reproducibility and accuracy between the scale and otolith methods.

Materials and Methods

Alewives, *Alosa pseudoharengus*, were taken daily from the commercial harvest throughout the fishing period for their otoliths and scales. The fish were taken to the laboratory, sexed, and measured for length and weight. About 10 scales were removed from the left side above the lateral line just posterior to the dorsal fin. The scales were cleaned and put into envelopes labeled with the length and sex of the alewife. In 1963, Rothschild described the alewife scale and characteristics of the annuli.

Otoliths were collected and stored as follows: A

[1]This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 89-304, as amended, Commercial Fisheries Research and Development Act, Project AFC-21-1.

transverse cut was made at the point of attachment of the operculum, which severed the head leaving some attachment of skin to the body. The head was then pulled away from the body removing the gills, leaving the skull clear of the gills and viseral blood. When time did not permit for further processing, all the heads from a day's sample were placed onto a tray and frozen for later analysis. For otolith removal, the head was held ventral side up and a transverse cut was made into the skull at the point of dorsal musculature attachment (Fig. 1a). A correct cut was sliced through the ends of the semicircular canals containing the sagitta otolith (Fig. 1b). Kornegay, in 1978, described the sagitta otolith that is used for age determination of the alewife.

Each otolith was extracted with microforceps, placed on absorbent paper, and rubbed lightly to remove any adhering tissue. After drying, otoliths were placed in depressions in black Plexiglas[2] trays and covered with Permount (see Libby 1982). Williams and Bedford (1974) described the growth and collection of otoliths and interpretation of otolith annuli in general. The Atlantic herring, *Clupea harengus*, otolith which is similar to the alewife otolith, was described by Watson (1964). He reported on the high validity of its use for aging and the high reproducibility of readings between readers.

Scales and otoliths were collected from 536 fish. Thirty-one fish were discarded because the otoliths or scales were unreadable or the shape of the otolith revealed that the fish was a blueback, *A. aestivalis*. Price (1978) explained the difference in otolith morphology between the two species. A final count of

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

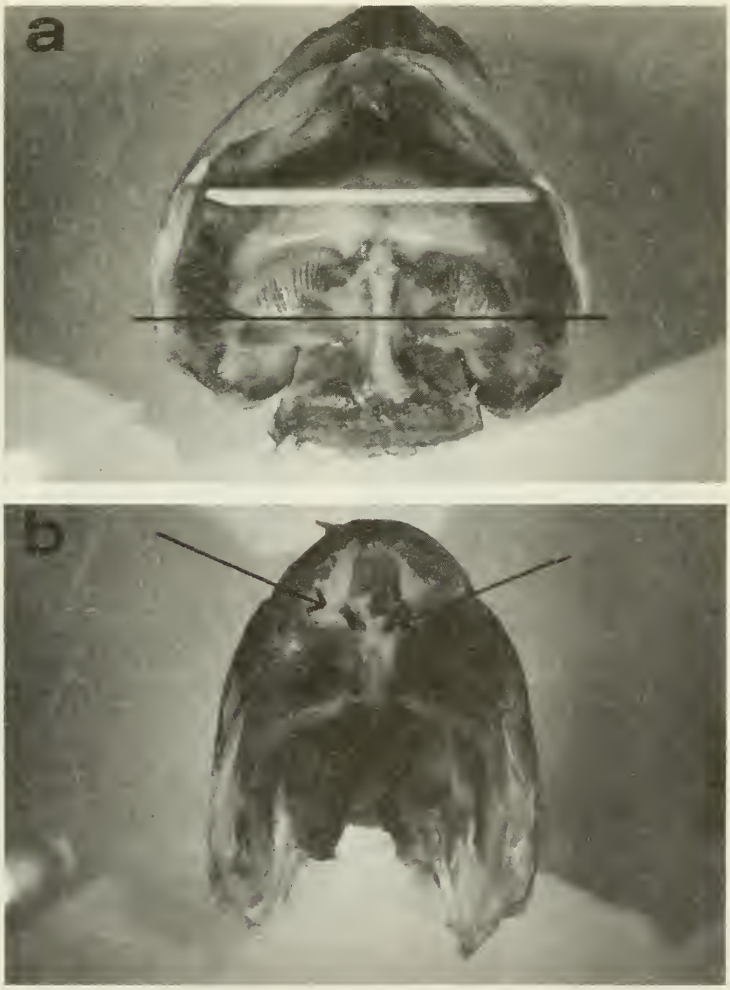


FIGURE 1.—a) Ventral side of head of *Alosa pseudoharengus*. Dark line shows musculature attachment to the skull where transverse cut is made. b) Section of skull cut away showing posterior ends of the semicircular canals containing the sagitta otoliths.

505 alewives was used for the analysis. Otoliths and scales were read using a binocular dissecting scope at 30×-60×.

Each otolith and scale for an age shown in Figure 2 was collected from the same fish. The otoliths were taken from the left side of the head and each scale was chosen for the best annuli appearance of all scales from that fish. The scale annuli shown are at the anterior portion of the scale that is normally covered by surrounding scales. The otoliths were photographed with a 35 mm camera mounted on a microscope at 11×.

Aging was done independently by two people (readers; subsequently referred to as R_1 and R_2). Ages derived from scales and otoliths by each reader were referred to as an age set. Scales and otoliths were read without knowledge of fish length or sex. A true age was established for each fish by reexamining scales and otoliths together with length and sex. The five age sets were compared to show 1) the precision of aging reproducibility (measurement of how close the ages are for two or more readings); and 2) the aging accuracy (age determinations compared with the true age).

Three analyses were used to evaluate precision and accuracy. Percent agreement (PA) compared two to three age sets to reveal what portion of the fish were aged alike between age sets. An index of average percent error (APE) developed by Beamish and Fournier (1981) was used to show the degree of variation between age sets. APE is expressed as

$$\frac{1}{N}\sum_{j=i}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}\right]$$

where N is the number of fish aged; R is the number of ways each is aged; X_{ij} is the ith determination of

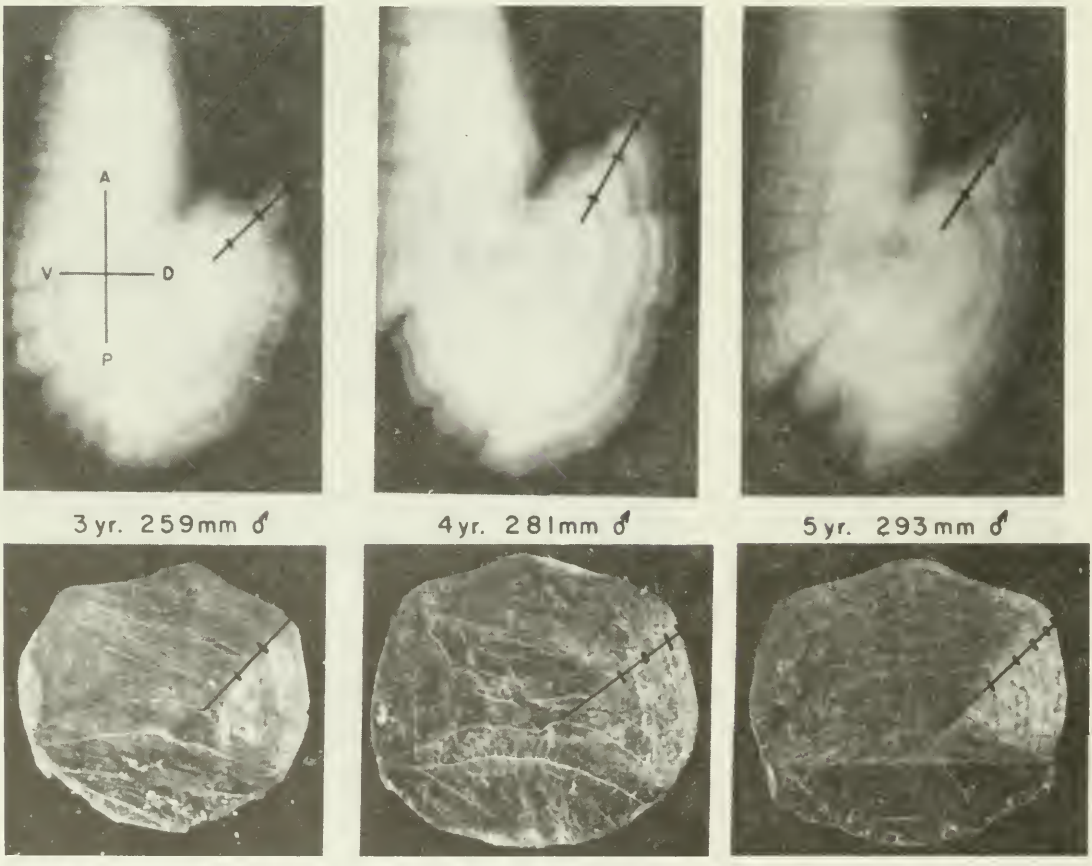


FIGURE 2.—Gross comparisons of otoliths and scales of alewives from ages 3 through 7. The otolith and scale were taken from the same fish for each age. The age-3 otolith shows: A - anterior; P - posterior; D - dorsal; and V - ventral orientation of the otoliths

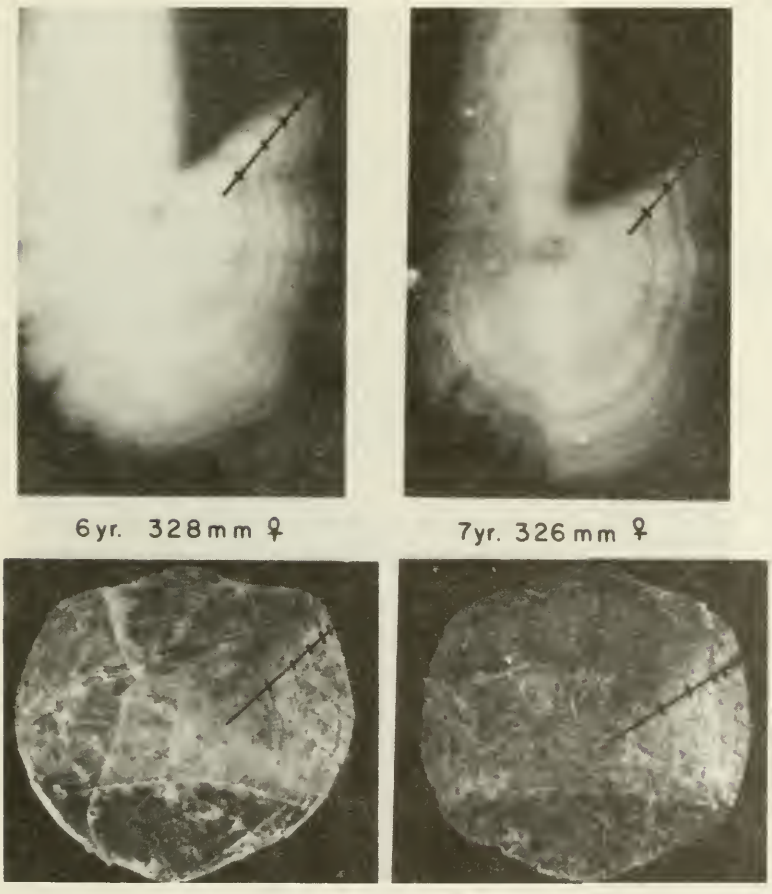
the jth fish; the X_j is the mean age calculated for the jth fish. The third method used the mean coefficient of variation (V) (Chang 1982). This was an alternative index to APE that provided a statistical test of reproducibility between agings. The coefficient was a measure of the standard deviation between all ages of fish divided by the mean age. The sum of the coefficients was then divided by the number of fish aged. PA, APE, and V are all expressed as percents.

The difference between PA and APE or V is that the former measures the actual agreement between age sets and the latter measures the amount of variation between age sets. Two treatments (a treatment was the comparison of two or more age sets) that had the same PA values might have differing degrees of variation and therefore different values of APE or V. The smaller the APE or V values, the less variation there was between age determinations.

Values for PA, APE, and V were computed for 10 treatments: scales vs. otoliths from R_1; scales vs. otoliths from R_2; scales from R_1 vs. R_2; otoliths from R_1 vs. R_2; scales from R_1 and R_2 vs. true age; otoliths from R_1 and R_2 vs. true age; male scales from R_1 vs. R_2; female scales from R_1 vs. R_2; male otoliths from R_1 vs. R_2; and female otoliths from R_1 vs. R_2. Treatments were also compared as to the relative sizes of the PA, APE, and V values.

Results

Figure 2 compares the physical appearance of otoliths and scales for ages 3 through 7. The photograph of the age-3 otolith shows its orientation as it lies in the sacculus. The dorsal side, including the anti-rostrum, shows the best contrast between the light opaque (summer growth) regions and the dark hyaline (winter growth) regions. The annular rings



in the sacculus. Lines drawn on the otoliths and scales show annular growth.

at this site are, for the most part, continuous and distinct. The annular markings on the scales are not as distinct or as sharp in contrast as on the otoliths. The scale annuli from the first three ages are well defined, but in ages 6 and 7 the outer annuli start to run together and the scale margin shows wear from resorption and deterioration. In contrast, the age-6 and -7 otoliths still reveal distinct annular rings.

PA, APE, and V values for all 10 treatments are presented by treatment comparisons in Table 1. The scale vs. otolith treatments were compared to determine how similar the two readers were in interpreting scale and otolith annuli. The PA values (82.6%, 80.4%) are relatively close to one another along with the values for APE and V. These values did reveal that R_1 had more agreement and less variability between aging scales and otoliths than did R_2. Table 1b shows a higher percentage agreement and less variability between R_1 and R_2 for otoliths than for scales.

Comparisons made between treatments of scales to true age and treatments of otoliths to true age are shown in Table 1c. The agreement of otolith ages to true ages was 10% greater and had half the variation of scale ages. Treatment comparison between male and female scale values were about the same (Table 1d), whereas the otolith values between sexes are quite different (Table 1e). The female otolith treatment had a higher PA value and lower APE and V values than did the male treatment.

Discussion

The scale vs. otolith treatment (Table 1a) revealed no real difference in the aging ability of each reader. There were also higher PA and lower V values for the treatment of otolith to true age (Table 1c). Therefore, the outcome for other treatments could be attributed to differences in the aging methods rather than the aging ability of the readers.

The results of the statistical tests (Table 1b) suggest that the method of estimating alewife ages from otoliths is superior to the method using scales. Ages derived from otoliths revealed a higher reproducibility and less variability than those obtained from scales. These differences between methods were inherent within the otoliths of female alewives, which provided the greatest accuracy and lowest variability (Table 1e) within all types of statistical comparisons.

Female alewives, at one time during their lives, possibly achieve a faster rate of growth than males. Cooper (1961), Havey (1961), and Libby (1982) showed that females are larger than males at age. This attribute of females would have the same effect on the growth of the otolith resulting in wider opaque zones with more distinct hyaline rings than male otoliths. Female scales would also have greater growth but possibly because of scale resorption and deterioration they were less easy to read than otoliths.

Other investigators have mentioned the ease of interpreting annuli of otoliths compared with scales, but have remarked that otoliths are less convenient to collect and store (Norden 1967; Kornegay 1978). The method presented in this paper was found to be more effective in obtaining both otoliths, unbroken, than the commonly used transverse cut made to the side of the head. The method of storage eliminated transferring and handling individual otoliths each time they were used. A disadvantage in using otoliths was that the fish had to be sacrificed. More care was required initially to obtain otoliths than scales, but the technique was quickly learned. The use of otoliths for aging alewives was more accurate and less subjective than aging with the use of scales.

Acknowledgments

I wish to thank Sherry Collins, Maine Department

TABLE 1.—Percent agreement (PA), average percent error (APE), and mean coefficient of variation (V) values for five treatment comparisons: a) scales and otoliths for R_1 against R_2; b) scales of R_1 and R_2 against otoliths of R_1 and R_2; c) scales of R_1 and R_2 and true age against otoliths R_1 and R_2 and true age; d) scales of R_1 and R_2 for males against scales of R_1 and R_2 for females; and e) otoliths of R_1 and R_2 for males against otoliths of R_1 and R_2 for females. S = scales; O = otoliths; 1 = R_1; 2 = R_2; A = true age.

	Treatment cmparisons									
	a		b		c		d		e	
	S_1O_1	S_2O_2	S_1S_2	O_1O_2	S_1S_2A	O_1O_2A	$S_1S_2♂$	$S_1S_2♀$	$O_1O_2♂$	$O_1O_2♀$
PA	82.6	80.4	85.0	89.0	78.8	87.7	84.0	85.8	86.5	92.2
APE	1.9	2.3	1.8	1.1	2.1	1.2	1.9	1.6	1.5	0.8
V	2.7	3.2	2.5	1.6	2.8	1.5	2.7	2.3	2.1	1.2

of Marine Resources, for her help and expertise in being a "reader"; Robert Guillard and James Rollins, Bigelow Laboratory for Ocean Sciences, for photographic services; and Vicki Averill, Maine Department of Marine Resources, for typing this manuscript.

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DAVID A. LIBBY

Maine Department of Marine Resources
Marine Resources Laboratory
West Boothbay Harbor, ME 04575

PROBABLE CAUSES OF THE RAPID GROWTH AND HIGH FECUNDITY OF WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN THE MID-COLUMBIA RIVER[1]

The introduction of walleye, *Stizostedion vitreum vitreum*, into the Pacific Northwest of the United States is not documented; however, they are now found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin[2]). The construction of dams has transformed the Columbia River from a free-flowing river into a series of low water-velocity impoundments with physical characteristics (Table 1) that closely match the model for ideal walleye habitat proposed by Kitchell et al. (1977a).

We studied basic life history factors of mid-Columbia River walleye for 2 yr to determine how well these exotic predators have adapted to their new environment. We found that our walleye grew at a rate approaching the highest previously reported, that they were highly fecund, and that they matured at an early age. We evaluated these high growth and reproductive rates against environmental and genetic variables. We believe these data will help to identify the ever increasing role of walleye in the aquatic ecosystem of the Columbia River and similar river-reservoir systems.

[1]Technical paper no. 6723, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, OR 97331.
[2]Durbin, K. 1977. News column. Oregon Department of Fish and Wildlife, P.O. Box 3503, Portland, OR 97208. Mimeogr., 3 p.

FIGURE 1.—Map of the lower and mid-Columbia River showing the locations of the major dams and the John Day pool study area where walleye were collected during 1980-81.

TABLE 1.—Summary of limnological data for the John Day pool of the Columbia River, from Hjort et al. (1981). All data collected in August 1979 except for surface temperatures, which were taken in 1981.

Characteristic	Range for John Day pool	Range for study area
Water velocity (m/s)	0.1-1.4	0.5-1.4
Secchi depth (m)	1.0-2.2	1.5-1.7
Dissolved O_2 (ppm) surface-bottom	16.0-8.0	14.0-10.0
Average surface temp. Apr.-July-Sept. (max.)	7.0°-24.5°-20.5°(24.8°)C	
Temperature profile surface-bottom	22.0°-20.8°C	21.0°-21.0°C
Pool width (km)	0.8-4.2	0.8-1.8
Mid-pool depth (m)	11-48	11-20
Pool length (km)	120	23

Methods

We collected walleye for this study in the first 23 km (tailrace) downstream of McNary Dam in the John Day pool of the Columbia River at lat. 45°55'N (Fig. 1). Walleye were collected from 2 April to 30 September 1980 and from 30 March to 30 September 1981. In 1980, we captured walleye with either a 38.1 × 1.8 m sinking gill net with 3.81, 5.08, 6.35, 7.52, and 10.16 cm variable stretch mesh, or a 76.2 × 3.7 m monofilament floating gill net with 15.25 cm stretch mesh. All gill net sets were of a maximum 2.5-h duration. In 1981 we used these gill nets and a 6.15 m electroshock boat with a 3,500-W generator and front-mounted electrodes, utilizing pulsed DC current of 1-4 A to capture walleye. Sampling was conducted in the day and night.

We recorded the fork length (FL, mm), weight (g), sex and whether or not the fish were sexually mature (Eschmeyer 1950), and removed a scale sample from beneath the tip of the left pectoral fin of each walleye. Many authors report difficulty using scales to determine the age of older walleye (Carlander and Whitney 1961; Campbell and Babaluk 1979); therefore, we took a subsample of sagitta (n = 86), which we preserved in 50:50 glycerine and water.

We mounted scales between two glass microscope slides and viewed them using a microfiche projector at 43×. We identified annuli using the criteria described by Carlander and Whitney (1961). We found that the easiest way to detect annuli on sagittae was to burn the whole otolith in a flame, immerse it in oil or alcohol, and examine it under a dissecting microscope. Reburning was often necessary until very distinct, dark annuli appeared. Christensen (1964) proposed a similar technique; however, he broke the burned otolith and examined the cross section. There was 92% agreement between at least one otolith reading and one scale reading so we terminated the collection of otoliths. We examined scales and otoliths twice and a person experienced in reading walleye scales (W. R. Nelson, U.S. Fish and Wildlife Service, Vancouver, WA) examined a subsample of scales (n = 63).

Age determinations for walleye collected in 1980 were based on either two scale readings, three scale readings, two scale readings and two otolith readings, or three scale readings and two otolith readings. All age determinations of walleye collected in 1981 were based on two scale readings. There was 90% agreement between at least two of the five possible age determinations for walleye collected in 1980, and 75% agreement between the two age determinations for walleye collected in 1981. After the final age determination, we measured the scale radius and scale length to each annulus (43×) at about 45° off of a straight line from the focus through the anterior field. In this area of the scale it was much easier to detect the annuli because of crowding and anastomosis of circuli in the lateral fields.

We back-calculated length at each annulus (i.e., year of life) assuming a straight line body-scale relationship (r^2 = 0.69) and using the Fraser-Lee method as recommended by Carlander (1982):

$$L_i = a + \frac{(L_c - a)}{S_c} S_i$$

where L_c = fish fork length at capture
L_i = calculated fork length at age i
S_c = scale radius at capture
S_i = scale measurement at annulus i
a = intercept of body-scale regression = 55 mm.

We converted these back-calculated fork lengths to total lengths (TL) using a conversion factor of 1.06 FL, which is the unweighted mean of the TL/FL relationships reported by Colby et al. (1979). This conversion allowed us to more easily compare our data with data from other areas.

During the spring 1981 spawning season, we removed the ovaries from 27 mature, but unspawned walleye. We preserved the ovaries in Bouin's solution and subsequently estimated the number of eggs by means of the gravimetric method recommended by Wolfert (1969). We performed regressions of life

history characteristics by use of an interactive statistical computer program.

Results

We sampled over 250 walleye in each year, and they varied in length from 208 to 765 mm FL (220-810 mm TL) (Fig. 2). The weight (WT)/length (FL) relationship for 324 walleye was best described by the equation:

$$\text{Log}_e \text{WT} = -11.426 + 3.010 \text{ Log}_e \text{FL} \ (r^2 = 0.966).$$

The slopes and intercepts of similar weight-length regressions for walleye collected in 1980 versus 1981 and males versus females were not significantly different ($F = 4.61$; $\alpha = 0.01$; df = 2; 247).

We had no difficulty detecting annuli in the scale samples from older walleye because of their rapid growth and apparently short life span (Table 2). Although females are larger than males in each year of life, the difference is not statistically significant until after the second year.

The mean fecundity of 27 walleye, between 520 to 764 mm FL and 1,720 to 5,905 g weight, was 82,900 eggs/kg body weight (Table 3). We found fecundity (FEC) linearly related to fish weight (WT):

$$\text{FEC} = -28{,}100 + 93.8 \text{ WT}, \quad r^2 = 0.969$$

and curvilinearly related to fork length (FL):

$$\text{Log}_e \text{FEC} = -8.4 + 3.2 \text{ Log}_e \text{FL}, \quad r^2 = 0.905.$$

A majority of males and females were mature by age III (Fig. 3); however, the maturity at fork length data show a more gradual increase than do the maturity

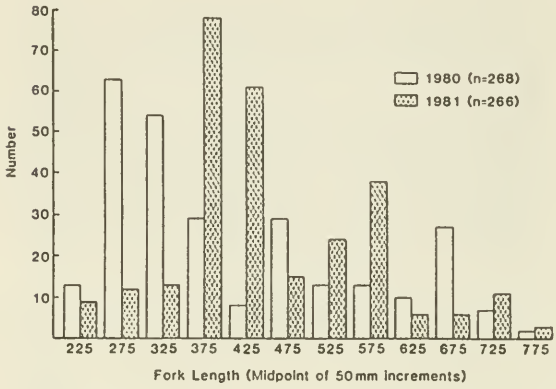

FIGURE 2.—Length-frequency distribution of walleye collected from the John Day pool of the Columbia River, April-September 1980-81.

TABLE 2.—Average back-calculated fork length (FL), SE, and annual growth increment for walleye collected in the John Day pool of the Columbia River, April-September 1980-81.

	Age							
	I	II	III[1]	IV[1]	V[1]	VI[1]	VII[1]	VIII
Males								
FL (mm)	241	363	434	484	533	562	596	
SE	2	3	6	7	9	10	7	
N (cumulative)	134	86	35	25	21	18	8	
increment (mm)	241	122	71	50	49	29	34	
Females								
FL (mm)	243	371	466	527	590	643	684	701
SE	2	3	4	4	5	5	6	11
N (cumulative)	197	150	122	95	69	57	28	8
increment (mm)	243	128	95	61	62	54	41	17
Combined[2]								
FL (mm)	244	368	458	515	575	623	664	701
SE	2	2	3	4	4	5	8	11
N (cumulative)	446	277	189	142	104	85	40	8
increment (mm)	244	124	90	57	60	8	41	37

[1]Females versus males significantly different, $P < 0.01$, Student's *t*-test.
[2]Includes some fish whose sex was not determined.

TABLE 3.—Fecundity of walleye from the John Day pool of the Columbia River, 30 March to 18 April 1981, compared with fecundities from Norris Reservoir, TN (Smith 1941), Lake Gogebic, MI (Eschmeyer 1950), and western Lake Erie (Wolfert 1969).

		Eggs/kg body weight[1]	
Location	*N*	Range[1]	Mean[1]
John Day pool	27	69,000-101,000	82,900 ± 1,550 (1SE)
Norris Reservoir		28,400-32,700	29,700
Lake Gogebic	34	57,900-67,800	61,800
Western Lake Erie	78	56,300-123,200	82,500

[1]Values converted from eggs/pounds body weight and rounded to nearest 100 eggs, except John Day pool.

data by age and, inexplicably, males were not 100% mature at any length (Fig. 3).

Discussion

The transplanted walleye population of the John Day pool of the Columbia River grows at a rate approaching the highest previously reported (Fig. 4). Concomitant with rapid growth these walleye are very fecund (Table 3) and mature at an early age (Fig. 3). We suggest that these life history characteristics result from the combination of a favorable temperature regimen and a nonlimiting food supply.

High growth rates are generally found in walleye populations of more southerly latitudes where higher temperatures and longer growing seasons occur. Figure 4 contains data from Norris Reservoir, TN (Stroud 1949), Lake Gogebic, MI (Eschmeyer 1950), Lac la Ronge, Saskatchewan (Rawson 1957); as well as the composite high and low length-at-age values reported by Colby et al. (1979). Relative to the latitude of the John Day pool (lat. 45°55′N), Norris Reservoir is south (lat. 36°15′N), Lac la Ronge is north (lat. 55°07′N), and Lake Gogebic is at approximately the same latitude (lat. 46°47′N). The mean growing degree-days (GDD) above 5°C (GDD >5°C)

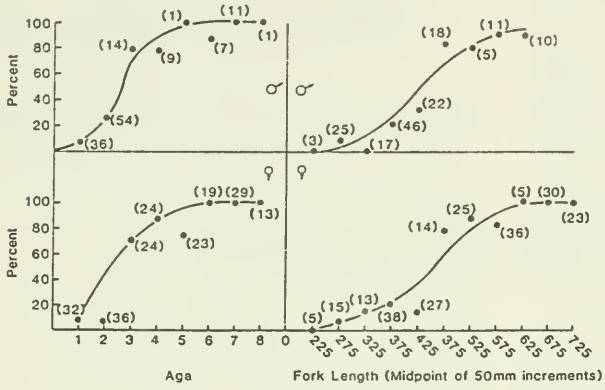

FIGURE 3.—Percent mature walleye by age and length and by sex for specimens collected in the John Day pool of the Columbia River, April-September 1980-81. Curves were drawn by eye. (Sample size in parentheses.)

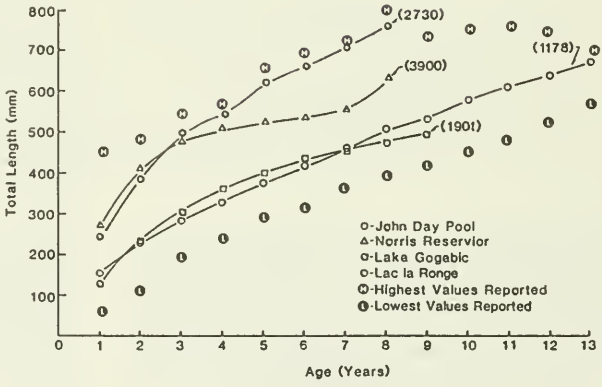

FIGURE 4.—Comparison of length-at-age for walleye from the John Day pool, Columbia River; Norris Reservoir, Tennessee (Stroud 1949); Lake Gogebic, Michigan (Eschmeyer 1950); Lac la Ronge, Saskatchewan (Rawson 1957) and the composite high and low values reported by Colby et al. (1979). Numbers in parentheses are the mean growing degree-days above 5°C, John Day value is from Anonymous (1969), all others are from Colby and Nepszy (1981).

(Colby and Nepszy 1981) for each area are included in Figure 4 as a measure of solar energy input to the system. Colby and Nepszy (1981) found that walleye growth was directly correlated to GDD >5°C and that the optimum range was from 2,500 to 4,000 GDD >5°C. While the GDD >5°C for the John Day pool is within this range, the walleye growth reported here is greater than would be predicted using this variable.

Water temperature may be the most important factor governing the growth of fishes (Brett 1979). Kitchell et al. (1977b) presented a bioenergetics model for walleye growth and indicated that thermal optima and maxima for weight specific consumption are 22°C and 27°C, respectively, and 27°C and 32°C, respectively, for weight specific respiration. Water temperatures in the John Day pool during the growing season remain at or near the thermal optimum for consumption and, perhaps more importantly, do not approach the thermal maxima for consumption or respiration (Table 1). Many northern lakes may not reach the thermal optima (Rawson 1957; Swenson 1977) and the southern lakes or lakes which stratify in the summer may exceed the thermal maxima (MacLean and Magnuson 1977) not only reducing consumption but increasing respiration. Dendy (1948) reported that in June 1944 the surface temperature of Norris Reservoir was about 30°C and that walleye appeared to prefer water temperature of about 24°C, even though these areas had oxygen concentrations <3.0 mg/L. Conversely, water temperature of Lac la Ronge did not exceed 20°C (Rawson 1957), well below the thermal optima.

Exceptions to the north-south trend in high walleye growth occur in systems of high exploitation (Forney 1965) and/or where there have been decreases in interspecific competition (Wolfert 1969; Forney 1977) which results in density dependent increases in growth rates. The quantity and quality of food are important factors in walleye growth (Kelso 1972; Kerr and Ryder 1977; Kitchell et al. 1977b) and fecundity (Colby and Nepszy 1981). Schupp (1978) looked at the growth of walleye from several areas within Leech Lake, MN, and found food of walleye from areas of highest average growth was almost totally young-of-the-year yellow perch, whereas small walleyes from slow growth areas had eaten mostly invertebrates and small minnows. We have found (Maule and Horton 1984) that about 99% by volume of Columbia River walleye stomach contents were fish (e.g., sculpins, suckers, cyprinids) and that 61% of walleye sampled contained food. Eschmeyer (1950) reported that 89% of the volume of stomach contents from Lake Gogebic walleye was fish, but he did not report percent empty stomachs. Dendy (1946) reported that Norris Reservoir walleye stomachs contained 99% fish by volume, but only 45% of the walleye examined contained food. Rawson (1957) studied Lac la Ronge walleye and reported that fish comprised 97% of the volume of stomach contents and that 39% of the walleye stomachs contained food.

Colby and Nepszy (1981) stated that age to maturity is indirectly correlated to growth, but that fecundity is probably a function of population density and food availability. They further suggested that the wide variability in walleye fecundities is a mechanism by which walleye can adjust production in response to environmental conditions. Table 3 includes fecundity data from Norris Reservoir (Smith 1941), Lake Gogebic (Eschmeyer 1950), and western Lake Erie (Wolfert 1969). Based on a comparison of growth, stomach content analysis, and fecundity, the mid-Columbia River walleye have a more favorable food supply than the other areas considered here.

Hackney and Holbrook (1978) suggested that there is a southern race of walleye that is characterized by rapid, large growth and short life span, and a northern race characterized by slow growth and long life span. They suggested that the pattern of rapid walleye growth seen after the impoundment of southern waters, followed by decreased growth rates some years later is due to a shift from the southern race to the northern race as the result of walleye stocking programs. The movements of young-of-the-year walleye downstream past Columbia River dams has been documented (Brege 1981). Assuming that this is a means by which walleye have colonized the Columbia River, it is biologically similar to impounding waters already containing walleye populations, in that new habitat is available for population growth. Although we cannot discount the possibility that the extreme life history characteristics reported here are the result of genetic stock differences, we suggest that they can more reasonably be explained by a favorable temperature regimen and an abundant, high quality food supply.

Acknowledgments

We thank Hiram Li and Carl Bond for their reviews of the manuscript. Funding was provided by the U.S. Army Corps of Engineers contract DACW 57-79-C-0067, the Oregon Agricultural Experiment Station, and the Milne Computer Center, Oregon State University, Corvallis, OR.

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Alec G. Maule

Oregon Cooperative Fisheries Research Unit
Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331

Howard F. Horton

Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331

BIOLOGICAL ASPECTS OF THE SPRING BREEDING MIGRATION OF SNOW CRABS, *CHIONOECETES OPILIO*, IN BONNE BAY, NEWFOUNDLAND (CANADA)

The occurrence of an annual (April-May) deep- to shallow-water breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, on the west coast of Newfoundland, has been documented by Hooper (in press). In addition to being the first record of this phenomenon in this species, his observations contradict some generally accepted conclusions regarding the species' reproductive biology. The most significant of these are that females undergo a terminal molt to maturity and do not mate in the hard shell condition (Ito 1967; Watson 1972; Takeshita and Matsuura 1980).

Little morphometric sampling data are included in Hooper's general description of the breeding migration. The purpose of this paper is to provide a more detailed description of various biological aspects of the phenomenon, such as size difference between paired males and females, and condition of the external egg masses, ovaries, and spermathecae during the breeding period.

Materials and Methods

Three hundred and three sexually paired snow crabs were collected during three field trips to Bonne Bay from 24 April to 29 May 1984 by scuba diving (10-30 m depth). Each pair was kept in a separate mesh bag. At the surface, each crab was measured to the nearest millimeter (maximum carapace width (CW)) and its shell condition (soft, new/hard, or old/hard) determined. The eggs of females were examined to determine their stage of development. Following this, males were tagged with Floy vinyl "T-bar" tags (Taylor 1982) and released, and females were either tagged and released, or retained for later examination of their ovaries and spermathecae in the laboratory.

Results

Size Distribution

Size distributions were unimodal for each sex but with no overlap in their carapace widths (Fig. 1). Males ranged from 89 to 140 mm ($\bar{x}$ = 116.4 mm) CW and females from 55 to 86 mm ($\bar{x}$ = 67.8 mm). Other than the fact that males were invariably larger than females, there was no discernible relationship between size of the male and size of the female with which it was paired (Fig. 2). Mean sizes of females paired with small, medium, and large size males were the same ($P < 0.005$, Bartlett's test of homogeneity of variance).

Male CW (mm) *Range*	*Female CW (mm)* *Range*	*Mean*	N
89-109 (small)	55-86	69.2	59
110-120 (medium)	59-86	69.6	136
121-120 (large)	59-84	70.9	108
		Total	303

The mean difference in carapace width between paired males and females increased from 21 mm at 89 mm male CW to 70 mm at 140 mm. Only 3 males in 303 pairs were smaller than 95 mm, the legal size limit.

Female Reproductive Condition

During the 24-27 April sampling period, 92% of the females carried full clutches of eyed eggs and the remainder had liberated all or most of the larvae (Table 1). By 7-11 May, 59% had empty brood pouches indicating that hatching was well advanced. However, during 22-25 May, 53% of the females were carrying full clutches of eyed eggs and only 39% had empty brood pouches. This increase in relative abundance of females with eyed eggs could have resulted from a return to deeper water of females that had liberated larvae or an influx of new animals from deeper water. Dead eggs were carried by 1.4% of females examined. All females dissected (77) had ripe (extrusion imminent) ovaries (Table 2); however, only two with partially extruded clutches

TABLE 1.—Summary of observations on external egg masses of female *Chionoecetes opilio* collected in Bonne Bay, Newfoundland, April-May 1984.

Sampling period	Eyed (%)	Larvae liberating (%)	Larvae liberated (%)	*N*
24-27 April	92	0	8	128
7-11 May	9	32	59	81
22-25 May	53	8	39	87

TABLE 2.—Summary of internal observations on female *Chionoecetes opilio* collected in Bonne Bay, Newfoundland, April-May 1984.

Sampling period	Ripe ovaries (%)	Spermatophores (%)			*N*
		Old only	Old and new	New only	
24-27 April	100	45.7	48.6	5.7	35
22-25 May	100	7.1	92.9	0	42

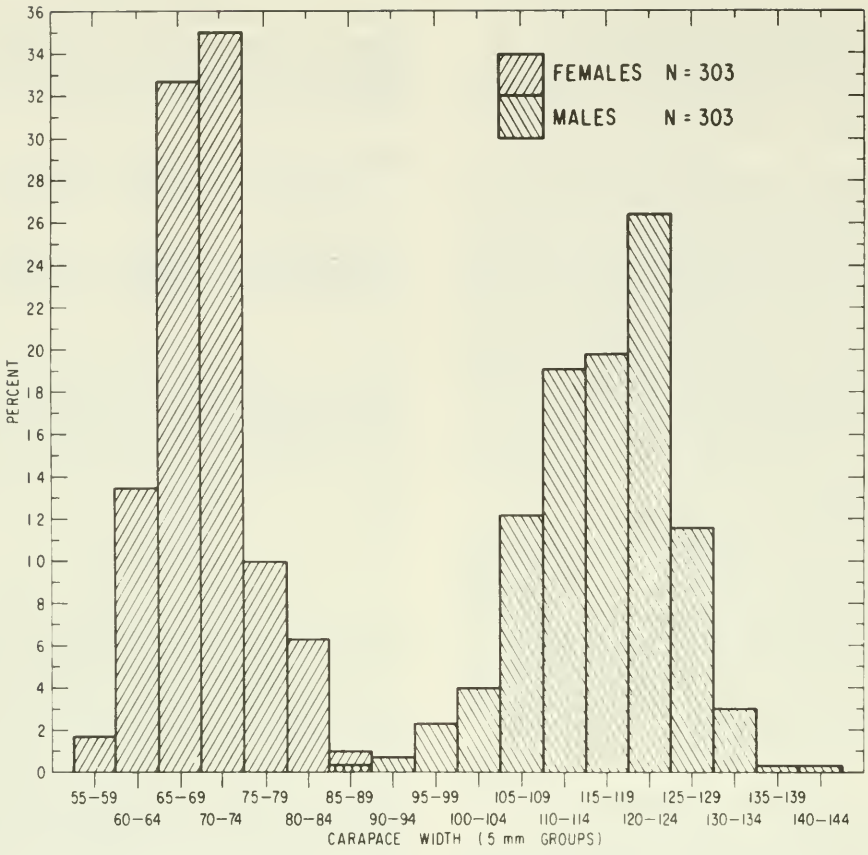

FIGURE 1.—Size-frequency distributions of male and female *Chionoecetes opilio* collected as pairs in Bonne Bay, Newfoundland, during April-May 1984.

of new eggs were found over the entire sampling period.

Females were observed with spermathecae containing both old and new spermatophores. In these, spermathecae were engorged with a very white glutinous material containing new spermatophores for three-fourths of their length, while the remaining one-fourth at the dorsal end of the organ was shrunken and contained a yellowish brown substance of a "waxy" consistency. Females which did not have new spermatophores had very small spermathecae which were entirely yellowish brown in color. This is very similar to that described for *Chionoecetes bairdi* by Paul (1982). While 97% of all females examined contained old spermatophores, those containing new spermatophores as well increased to 92.9% from 48.6% between 24 April and 25 May (Table 2). Two specimens contained new spermatophores only and all had old epizooite-encrusted shells. Thirty-six percent of the females with new spermatophores carried full clutches of eyed eggs.

Diving during 28-31 May revealed that all crabs had left the sampling area.

Discussion

Small numbers of grasping, male/female pairs of *C. opilio* and *C. bairdi* have been observed in shallow water elsewhere. Ennis (Unpubl. data) found five pairs and Hooper (Unpubl. data) found three pairs of *C. opilio* in Bonavista Bay and Placentia Bay, Newfoundland, respectively. Donaldson (1975) reported two pairs of *C. bairdi* in Alaska. However, nothing comparable with the magnitude of the breeding migration of *C. opilio*, observed in Bonne Bay, Newfoundland, has been reported for other areas. There is considerable scope for speculation on the ecological significance of this migration. Although about half the females examined just prior

to their departure from the shallow (<35 m) sampling depths in 1984 still had full clutches of eyed eggs, liberation of a large proportion of larvae in shallow water may enhance chances for larval survival overall. At the time of the migration, bottom temperatures in Bonne Bay at depths beyond 35 m are probably 0°C or lower [deep water temperatures are not available for Bonne Bay but Squires et al. (1971) reported temperatures <0°C at depths beyond 30 m in early June in North Arm, Bay of Islands, about 40 km to the south]. Release of larvae in shallow, warmer water (temperature was 3°C at 30 m during 7-11 May) would considerably reduce the degree of thermal shock associated with larvae swimming to the surface. The rate of embryonic development would likely be increased also, resulting in earlier larval release.

In the development of a management strategy for *C. opilio* stocks on the Atlantic coast of Canada, a key assumption has been that, despite high levels of exploitation, reproductive potential in a stock remains at prefishery levels. The basis for the assumption is that females are protected from exploitation by the 95 mm CW minimum legal size because they do not grow to that size and also that males mature at sizes much smaller than 95 mm CW. In a recent review, following more than 15 yr of heavy fishing in some areas, there was no evidence to indicate that the assumption was invalid (Elner and Robichaud 1983). However, the observations presented here suggest that a large size differential between the male and female of a pair is an important element of behavioral interactions during breeding activity. It is possible that males smaller than 89 mm CW (the smallest male observed paired with a female), even though physiologically mature, may be less likely to mate successfully in competition with large males.

Males and females appear to be segregated over most of the year (Hooper in press). Observations on the east coast of Newfoundland indicate that large males occur mainly on muddy bottom in deep water whereas females and small males occur on sand-gravel or rocky bottom somewhat shallower (Miller and O'Keefe 1981). In the breeding migration which occurs in Bonne Bay, Hooper (in press) suggested that males leave the deeper water area after selecting a mature female which is carried to the shallow water breeding area. Males retain possession of individual females for extended periods (Hooper in

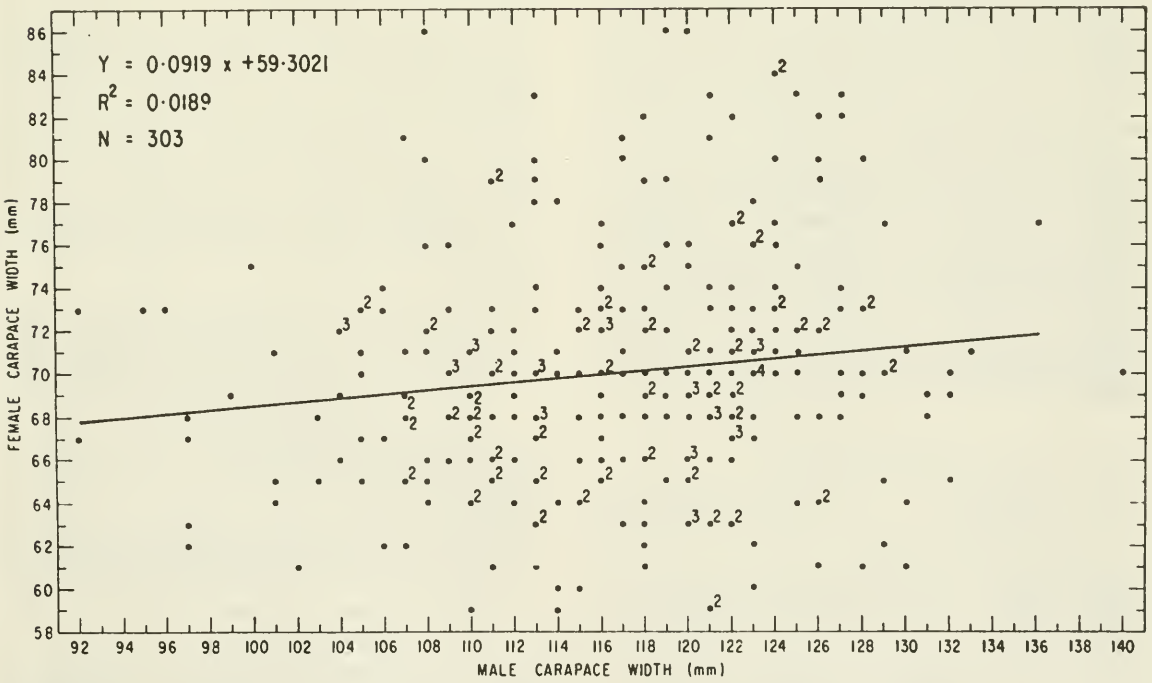

FIGURE 2.—Regression of female carapace width on male carapace width for pairs of *Chionoecetes opilio* collected in Bonne Bay, Newfoundland, during April-May 1984. Numbers adjacent to points indicate more than one observation. Slope of the regression is not significant (P = 0.017).

press) (possibly up to 2 mo) during which time the female is held by and dependent on the male. In laboratory studies on *C. bairdi*, Paul and Adams (1984) demonstrated that multiparous females are receptive to mating for periods ranging from <1 to 7 d after all their eggs have hatched. In fact, they reported that only one ovigerous female mated successfully during their study.

In the Gulf of St. Lawrence, male snow crabs mature within the 50-65 mm CW size range (Powles 1968; Watson 1970); however, in the sampling reported here, only 3 males from the 303 pairs examined were smaller than the 95 mm CW minimum legal size, the smallest being 89 mm. Except for these, even solitary males of this size and smaller were absent from the area indicating that competition for females had occurred in deeper water. This snow crab population appears to be small and is isolated from populations elsewhere in the Gulf of St Lawrence by the 35 m deep sill at the mouth of Bonne Bay. This area has not been fished commercially and at present the population is considered to be in the virgin state. Hooper's (in press) observations indicated there is keen competition between single males and males already paired with a female for possession of the female. Under prefishery conditions this competition can be expected to eliminate small males from participating in breeding activity. Adams (1982) demonstrated that multiparous female *C. bairdi* resisted mating attempts by small males, and when males of significantly different sizes competed for the same female, the larger male was invariably successful. Small numbers of the largest of the sublegal (<95 mm CW) male *C. opilio* appear to be capable of competing and mating successfully. However, it is presently unknown whether males smaller than those observed are capable of successful mating with multiparous females in the absence of competition from large males and, if they are not, whether there are sufficient numbers of large sublegal males to maintain full reproductive potential in a heavily fished population.

Acknowledgments

We are indebted to P. O'Keefe, G. Badcock, and D. Keats for assistance with field work, particularly diving, and to P. Collins, as well as P. O'Keefe and H. Mullett for assistance with data analysis and drafting.

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D. M. Taylor

Fisheries Research Branch
Department of Fisheries and Oceans

P.O. Box 5667
St. John's, Newfoundland A1C 5X1, Canada

R. G. Hooper

NICOS/Biology Department
Memorial University of Newfoundland
St. John's, Newfoundland A1B 3X9, Canada

G. P. Ennis

Fisheries Research Branch
Department of Fisheries and Oceans
P.O. Box 5667
St. John's, Newfoundland, A1C 5X1, Canada

FEEDING, DIET, AND REPEAT SPAWNING OF BLUEBACK HERRING, *ALOSA AESTIVALIS*, FROM THE CHOWAN RIVER, NORTH CAROLINA

Current knowledge of the frequency of feeding among spawning blueback herring, *Alosa aestivalis* Mitchill, is limited. Other aspects of the blueback herring's life history have been more extensively studied: feeding of juveniles (Davis and Cheek 1966; Nichols 1966; Burbidge 1974; Domermuth and Reed 1980; Crecco and Blake 1983), distribution at sea (Hildebrand 1963; Holland and Yelverton 1973[1]; Neves 1981), and spawning range (Bigelow and Schroeder 1953; Hildebrand 1963; Scott and Crossman 1973). However, determination of the occurrence of feeding by adults in freshwater has received little attention despite the fact that spawning bluebacks are common in rivers from southern New England (Bigelow and Schroeder 1953) to the St. Johns River, FL (Hildebrand 1963). Throughout this extensive range only Frankensteen (1976) has studied feeding among adult bluebacks in freshwater. Furthermore, no attempt has been made to correlate feeding with length, weight, and sex of individual fish, distance upstream, or the number of seasons a blueback has spawned.

The objective of this study is to enhance our knowledge of the freshwater feeding of blueback herring. In this paper I describe the occurrence of feeding, diet, and percentage of repeat spawning among adults collected in the Chowan River, NC. I also examined, by multiple regression analysis, the relation between feeding activity in freshwater and length, weight, sex, the number of repeat spawnings, and the distance travelled upstream.

Materials and Methods

Collection of Data

Bluebacks were collected at two sites in the lower Chowan River system during April 1980 and 1981. Williams' Fishery, where five collections were made in 1980, is located on the lower Meherrin River near its junction with the Chowan River, 90 km upstream from the Chowan River's mouth. Rocky Hock Creek, where bluebacks were sampled twice in 1980 and once in 1981, is roughly 20 km from the mouth of the Chowan River. Bluebacks at Williams' Fishery were still migrating upstream while those at Rocky Hock Creek, a known spawning ground,[2] were preparing to spawn.

Bluebacks were caught in chicken-wire dip nets and fixed gill nets with 58 mm stretched mesh at Rocky Hock Creek. A drift gill net of similar mesh size and a haul seine were used at Williams' Fishery. None of the fish collected had spawned yet.

Bluebacks were measured, weighed, and sexed, and scales were removed for aging. The foregut and midgut regions of the stomach anterior to the pyloric caeca were removed and placed in 15% Formalin[3] within 10-15 min of capture.

Stomach contents were examined in the laboratory under a dissecting scope. First, fullness of the foregut and midgut, which are separate sections, was estimated visually following Hynes (1950) and Yoshiyama (1980). Five levels of fullness were used: half full (1/2), full (1), and distended with food (2) (as in Yoshiyama 1980), plus one quarter full (1/4), and empty or with traces of food (0). Contents of each section were then placed in a petri dish, identified, and counted. Also, the presence or absence of prey items was noted.

Scales were viewed at 50× through an EPO LP-2 Profile Projector and marks were interpreted following Marcy (1969).

[1]Holland, B. F., Jr., and G. F. Yelverton. 1973. Offshore anadromous fish exploratory fishing program. Completion report, Project AFC-5, 123 p. North Carolina Department of Natural and Economic Resources, Division of Commercial and Sports Fisheries, Raleigh, NC 27611.

[2]S. Winslow, North Carolina Division of Marine Fisheries, Elizabeth City, NC 27909, pers. commun. February 1980. S. Winslow had determined the previous year (1979) that blueback herring collected at this site on Rocky Hock Creek were spawning. Also, a dam upstream prevented blueback herring from moving any further than 150 m above my collection site.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Statistical Analysis

To obtain a single index of stomach fullness, values for the foreguts and midguts were combined by using a weighted average. In calculating mean volumes each gut section was assumed to be approximately cylindrical. The foregut to midgut volume ratio, determined from five randomly chosen stomachs, was 3.16:1. The following equation was used to calculate the overall gut fullness:

$$\frac{F \times 3.16 + M}{4.16}$$

with F and M representing the foregut and midgut values, respectively.

A multiple regression (General Linear Model-Statistical Analysis Systems) was initially employed to determine which of the variables collected for each fish (i.e., distance upstream, length, weight, sex, and number of repeat spawnings) was most strongly correlated with stomach fullness, the dependent variable. Significant variables identified through multiple regression analysis were further analyzed with chi-square and F-tests.

Results

Presence of Food

Nearly all (91 of 103 or 88%) fish sampled in April 1980 contained food (Table 1) as did all 15 fish collected in April 1981. High percentages of the fish collected on each date in 1980 had food in their stomachs (Table 1). About 53% (48 of 91) of the bluebacks in 1980 (Table 1) and 73% (11 of 15) of the bluebacks in 1981 had either foregut and/or midgut fullnesses of 1/4 or greater. Approximately half of the fish from each date in 1980, with the exception of 13 April, had either foregut and/or midgut fullnesses of 1/4 or greater (Table 1).

Diet

The diet of the bluebacks collected in 1980 at both sites was composed of zooplankters, benthos, and terrestrial insects (Table 2). Chydorid cladocerans were the only zooplankters consumed in large numbers at either location (Figs. 1, 2). Insects, which accounted for 8.1% of the organisms consumed, occurred in about half of the fish. Ephemeroptera (*Baetis*), Coleoptera (Dytiscidae), and Heleidae larvae, as well as chironomid larvae and pupae, were the most conspicuous of the identifiable benthic insects. Most insects, benthic and terrestial, were unidentifiable. Chironomids occurred more frequently than other insect groups, but they accounted for only 2.7% of the total prey items. Several terrestrial insects were found in stomachs of bluebacks, particularly at Williams' Fishery. Insects, both benthic and terrestrial, increased in importance with time at Williams' Fishery, reaching about 22% during later collections (Fig. 1). Insects represented a smaller proportion of the diet at Rocky Hock Creek (Fig. 2). Fish eggs (probably from alewives or bluebacks), which occurred in the stomachs of several bluebacks in 1980 (Figs. 1, 2), were the most abundant food item in that year although their importance decreased with time. Varying amounts of sand and detritus occurred in many stomachs.

In 1981 the diet of bluebacks from Rocky Hock Creek was much less diverse (Table 3). Cladocerans, the predominant prey items, comprised 84.1% of the diet. Almost half of the prey items were daphnid

TABLE 1.—Incidence of feeding and stomach fullness in male and female blueback herring collected at Williams' Fishery (WF) and Rocky Hock Creek (RH) during April 1980.

Station and date of collection	No. fish collected per station	No. males (M) and females (F)		No. fish (*n*) with animal matter in stomach		No. of fish with ≥1/4 fullness for the foregut, midgut or both							
						Males			Females			Males + Females	
	N	M	F	*n*	% *F*	Fore	Mid	Both	Fore	Mid	Both	Total	% *N*
WF-4-5-80	16	8	8	12	75.0	0	1	0	1	2	3	7	43.6
RH-4-6-80	9	3	6	9	100.0	0	0	0	2	1	2	5	55.6
WF-4-7-80	17	8	9	15	88.2	1	3	0	0	2	3	9	52.9
WF-4-11-80	17	10	7	15	88.2	2	2	0	1	2	1	8	47.1
RH-4-12-80	7	6	1	7	100.0	1	1	0	0	0	1	3	42.9
WF-4-13-80	23	9	14	20	87.0	2	1	0	0	4	1	8	34.8
WF-4-19-80	14	10	4	13	92.9	0	5	0	0	2	1	8	57.1
Total	103	54	49	91	88.4	6	13	0	4	13	12	48	

cladocerans (Table 3). Few copepods were consumed, although they occurred in about half the fish. Ostracods were important numerically and in occurrence, as were daphnid ephippia. Benthic prey, terrestrial insects, fish eggs, detritus, and sand were rare.

TABLE 2.—Diets of 103 blueback herring collected at Williams' Fishery and Rocky Hock Creek during April 1980.

Prey taxon	Frequency of occurrence: No. of fish observed in	%	Proportions of prey items in diet: No. of prey	%
Copepoda				
Calanoida	1	1.0	1	(1)
Harpacticoida	5	4.9	12	0.4
Cyclopoida	35	33.9	80	2.8
Unidentifiable	7	6.8	21	0.7
Cladocera				
Chydoridae	61	59.2	839	29.6
Other families	14	13.6	26	0.9
Ostracoda	15	14.6	58	2.0
Insecta				
Miscellaneous	54	52.4	133	4.7
Diptera				
Chironomidae larvae	25	24.3	67	2.4
Chironomidae pupae	5	4.9	7	0.3
Other families	12	11.7	20	0.7
Oligochaeta	1	1.0	1	(1)
Mollusca				
Sphaeriidae	7	6.8	21	0.7
Fish eggs	43	41.8	1,273	44.9
Bryozoan statoblasts	20	19.4	178	6.3
Colonial hydrozoan pieces	16	15.5	96	3.4
Hydracarina	5	4.9	5	0.2
Total			2,838	100.0

[1]<0.1%.

TABLE 3.—Diets of 15 blueback herring collected at Rocky Hock Creek on 18 April 1981.

Prey taxon	Frequency of occurrence: No. of fish observed in	%	Proportions of prey items in diet: No. of prey	%
Copepoda				
Calanoida	5	33.3	8	0.1
Harpacticoida	7	46.6	7	0.1
Cyclopoida	7	46.6	23	0.4
Cladocera				
Daphnidae	15	100.0	3,191	48.7
Daphnidae ephippia	12	80.0	1,825	27.9
Chydoridae	13	86.6	493	7.5
Bosminidae	2	13.3	5	(1)
Ostracoda	13	86.6	929	14.2
Insecta				
Miscellaneous	5	33.3	6	0.1
Diptera				
Chironomidae larvae	5	33.3	8	0.1
Fish eggs	1	6.6	7	0.1
Bryozoan statoblasts	11	73.3	42	0.6
Hydracarina	3	20.0	3	(1)
Fish larvae	1	6.6	1	(1)
Total			6,548	99.8

[1]<0.1%.

Number of Repeat Spawnings

About 85% (87 of 103) of the fish in 1980 and 71% (10 of 14) in 1981 had spawned before (Table 4). Although some bluebacks in 1980 had spawned as many as six times, most (72%) had spawned only once or twice before (Table 4). Almost equal numbers of males (44) and females (43) were repeat spawners in 1980.

TABLE 4.—Number of previous years that 103 blueback herring collected at Williams' Fishery and Rocky Hock Creek during April 1980 had spawned.

	No. of years spawned					
	1 (first time)	2	3	4	5	6
Male	10	25	14	3	1	1
Female	6	22	13	6	2	0
Total	16	47	27	9	3	1

Relation Between Feeding Activity and Length, Weight, Sex, Number of Repeat Spawnings, and Distance Upstream

Sex was the only independent variable that contributed significantly to variance in feeding rate (Table 5). Female bluebacks fed more actively than males. The full model explained only 21% of the variance in gut fullness but this was significant ($F = 2.87, P > F = 0.005$, 102 df). The near significant contributions of length and weight to the reduction of variance in the model is believed to have resulted primarily from sex related differences in mean size ($\bar{x}$ length females = 305.1 mm, $\bar{x}$ length males = 289.4 mm; $\bar{x}$ weight females = 258.0 g, $\bar{x}$ weight males = 212.5 g). Further analysis of the feeding activity of male and female bluebacks with a chi-

TABLE 5.—Summary of the contribution of each of the independent variables to the multiple regression model for data from 103 blueback herring collected in 1980. Type IV F values and probability levels are shown. $P < 0.05$ significance level used.

Independent variable	F value	Probability
Site	2.64	0.1078
Sex	7.14	0.0089
No. of repeat spawnings	1.65	0.1818
Length	3.85	0.0527
Weight	3.81	0.0540

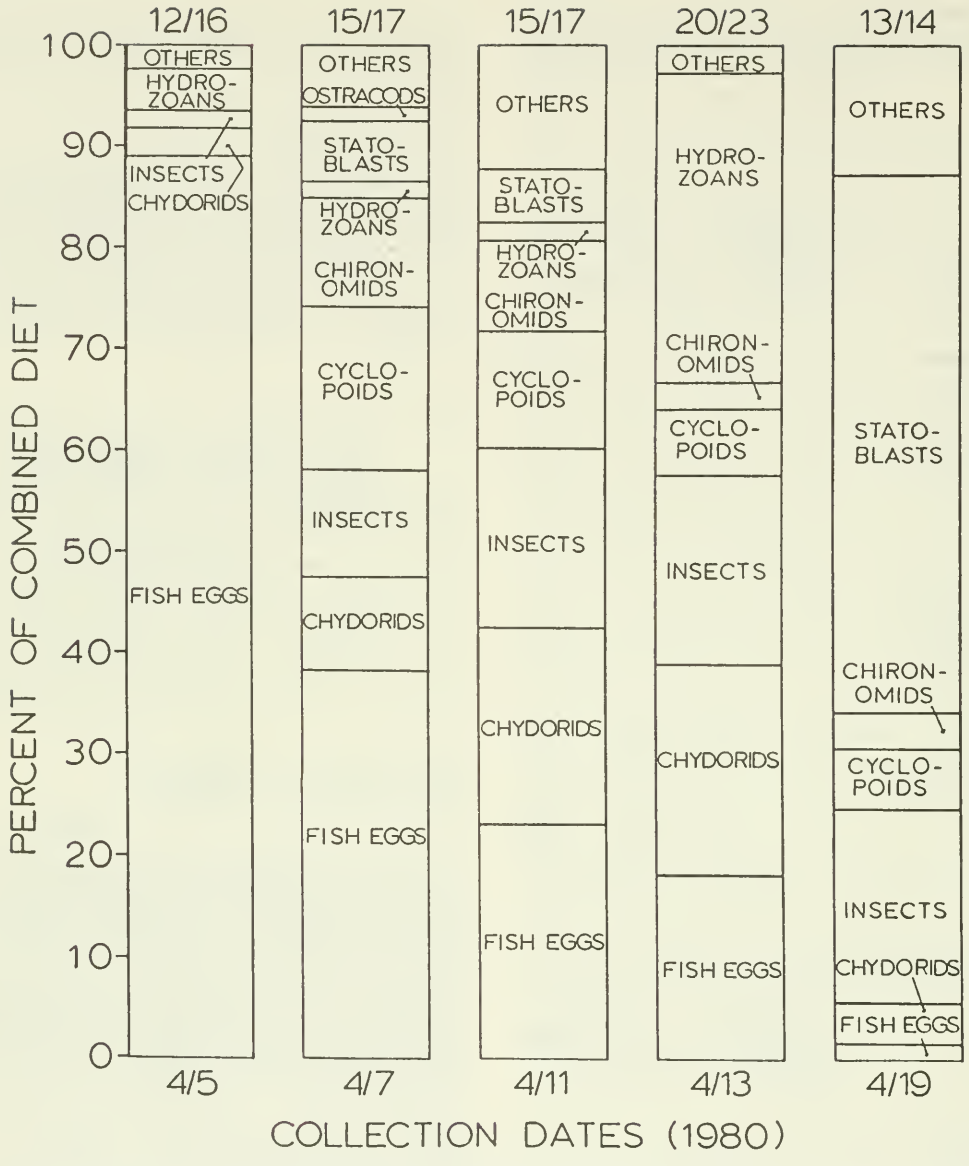

FIGURE 1.—Changes in the composition of the combined diet (both males and females) over the five collection dates at Williams' Fishery in April 1980. Numbers above each bar graph indicate number of stomachs with food/total number of stomachs examined.

square 2 × 2 contingency table also found significantly greater levels of feeding activity among females (χ^2 value = 5.86, $P < 0.025$). The difference in 1980, however, may depend on site. More females had stomach fullnesses ≥1/4 than males at Rocky Hock (χ^2 value 6.349, $P < 0.025$), but the difference was not significant at Williams' Fishery.

For the three most abundant food items females consumed significantly greater numbers of chydorid cladocerans ($F = 6.02$, $P > F = 0.0001$), insects ($F = 7.64$, $P > F = 0.0001$), and fish eggs ($F = 90.15$, $P > F = 0.0001$) than males in 1980.

Discussion

Blueback herring spawning in the Chowan River do not stop feeding during their freshwater migrations. Williams' Fishery and Rocky Hock Creek are

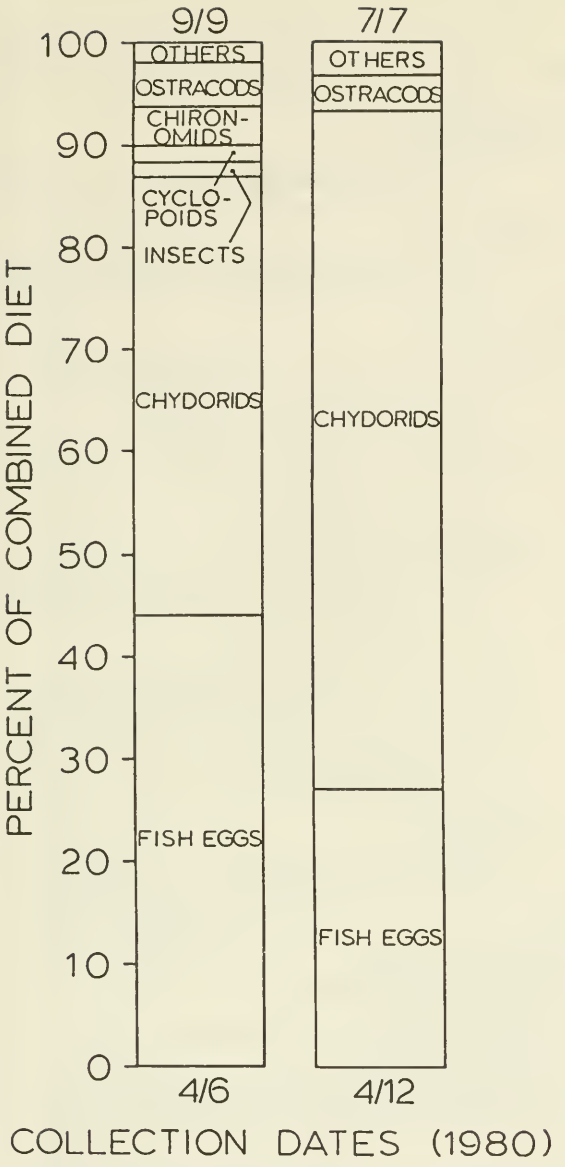

FIGURE 2.—Changes in the composition of the combined diet (both males and females) over the two collection dates at Rocky Hock Creek in April 1980. Numbers above each bar graph indicate number of stomachs with food/total number of stomachs examined.

too far from the estuary for bluebacks to travel to saltwater for daily feeding. It is important to note, also, that the interface between freshwater and saltwater often extends far out into Albemarle Sound due to the spring discharge of both the Chowan and Roanoke Rivers. This was the case in the spring of 1980.[4] Moreover, the prey were exclusively of freshwater origin. There is, therefore, little doubt that these bluebacks were feeding in freshwater.

The wide diversity of food items consumed was unexpected since bluebacks have previously been reported to be primarily planktivorous (Bigelow and Schroeder 1953; Hildebrand 1963). The limited 1981 data suggest that prey other than zooplankters are consumed infrequently if sufficient zooplankters (or large zooplankters such as *Daphnia*) are present. However bluebacks are also capable, as the 1980 data demonstrate, of foraging opportunistically on other riverine fauna and terrestrial insects, which could also explain Frankensteen's (1976) unusual finding that chironomids were the dominant prey of blueback herring in the Tar River. Consumption of benthic prey probably accounts for the presence of detritus and sand in the guts.

My data show a difference between male and female feeding activity. There are two possible explanations for this difference. First, females may require more energy than males during the spawning migration thus they consume more prey. Neither this study nor other studies of bluebacks have produced data to either support or refute this idea. However, moderate to severe weight loss is common among other spawning anadromous fishes (e.g., Atlantic salmon, American shad) with females suffering greater weight loss than males (Belding 1934; Chittenden 1976; Glebe and Leggett 1981). Glebe and Leggett (1981) found that development of ovaries in female shad required more energy and time than the male shads' testes. Consequently, female shad entering freshwater, particularly southern rivers, often do not have fully developed ovaries. Thus, not only must females expend energy for swimming but for gonad development as well. The same difference in gonad development may exist between male and female bluebacks and could explain the different levels of feeding activity observed in this study.

The second explanation for the difference in feeding activity is that all bluebacks, regardless of sex, stop feeding while spawning. However, males might remain on the spawning grounds longer than females. Thus, if females leave the area immediately after they spawn and are replaced by newly arrived females with relatively full guts, this could cause the gut samples to be biased. This explanation appears to be ruled out by the 1981 data, however, since half the fish with stomachs $\geq 1/4$ full collected at Rocky Hock were males.

While previous researchers have found food in bluebacks' stomachs (Williams et al. 1975 as cited

[4]R. Holmes, Department of Natural Resources and Community Development, Division of Environmental Management, Raleigh, NC 27611, pers. commun. March 1984.

in Rulifson et al. 1982; Frankensteen 1976), my finding of a regular occurrence of significant volumes of food in blueback stomachs is unprecedented. Further research is needed to determine the extent to which feeding in freshwater is common among spawning bluebacks in other river systems, and possibly other anadromous species, and to determine if a relationship exists between freshwater feeding and spawning energetics.

Acknowledgments

I am grateful to Seth Reice and Edward Kuenzler for providing assistance, materials, and workspace for this study. I also wish to thank Jerry Diamond, Seth Reice, William Leggett, Angela Arthington, Rob Edwards, Brad Foster, and three anonymous reviewers for their careful readings of the manuscript. Assistance from Mr. and Mrs. Williams and the staff of Williams' Fishery, Sara Winslow, Harrel Johnson, and Michael Street of the North Carolina Division of Marine Fisheries, David Hammer, Chris Nations, Ernie Patterson, and Diana Hyland, as well as thought-provoking discussions with many other people, is greatly appreciated.

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Robert P. Creed, Jr.

Department of Biology
University of North Carolina
Chapel Hill, NC 27514
Present address:
Department of Zoology
Michigan State University
East Lansing, MI 48824

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30. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838. By Sandra E. Shumway, Herbert C. Perkins, Daniel F. Schick, and Alden P. Stickney. May 1985, iv + 57 p., 46 figs., 36 tables.

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ERRATA

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Epperly, Sheryan P., and Walter R. Nelson, "Arithmetic versus exponential calculation of mean biomass," p. 446-448.

Page 446, left column, equation should read: $\bar{B}_t = \frac{B_t + B_{t+1}}{2}$

Page 446, right column, equation should read: $\bar{B}_t = \frac{\bar{B}_t\,(e^{G_t - Z_t} - 1)}{G_t - Z_t}$

447, left column, line 1, correct to read:

recruit. In one, $\bar{B}_t$ was computed arithmetically,

Page 447, right column, line 3, correct to read:

F-multiples and ages of entry, when $\bar{B}_t$ was cal-

Page 447, Figure 1, second line, correct to read:

when $dt = 1.0$ and $B_t = 1.0$, DELTA $= B_t(\bar{B}_{t,\,\mathrm{exp}} - \bar{B}_{t,\,\mathrm{arith}}) = B_t * \{0.0061 + 0.0037\,(G_t - Z_t) -$

Page 448, paragraph 1, line 8, correct to read:

ing a need to minimize the $G_t - Z_t$ difference if $\bar{B}_t$

Page 448, paragraph 1, last line, correct to read:

ommend that $\bar{B}_t$ be calculated exponentially.

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Fishery Bulletin	3 6 6 - 3 7 0	18 Sept. 1985
3. FREQUENCY OF ISSUE	**3A. NO. OF ISSUES PUBLISHED ANNUALLY**	**3B. ANNUAL SUBSCRIPTION PRICE**
Quarterly	4	$21.00

4. COMPLETE MAILING ADDRESS OF KNOWN OFFICE OF PUBLICATION *(Street, City, County, State and ZIP+4 Code) (Not printers)*
Scientific Publications Office, NMFS
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5. COMPLETE MAILING ADDRESS OF THE HEADQUARTERS OF GENERAL BUSINESS OFFICES OF THE PUBLISHER *(Not printer)*
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